Ecology of Three Species of *Euchaeta* (Copepoda: Calanoida) in the Coastal Waters of Hong Kong

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Ecology of Three Species of *Euchaeta* (Copepoda: Calanoida) in the Coastal Waters of Hong Kong

submitted by YAU, Yee Wa Eva

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ABSTRACT

Predatory copepods of the genus *Euchaeta* are widely distributed in most of the subtropical and tropical waters in the world. In the coastal waters of Hong Kong and southern China, this genus includes some of the most abundant and largest predatory copepods. My thesis research examines the geographical distribution, diel vertical migration and feeding impact of *Euchaeta* in two bays in the subtrophical coastal waters of eastern Hong Kong. Three species of *Euchaeta* occur in the study area. *E. concinna*, the dominant species in terms of abundance, comprise >70% of the total population of copepods of the genus *Euchaeta*, while *E. rimana* and *E. plana* are less abundant. All three species show distinct seasonality in occurrence and reach peak densities in winter and/or spring. The lack of clear patterns in cohort development in

Euchaeta populations suggests that all three species are not indigenous to local waters, but are transported into the area by ocean currents from neighboring oceans. Distributions of adults and copepodids of all *Euchaeta* species are restricted to Mirs Bay. Tolo Harbour is an important nursery ground for several species of commercially important fish in winter and early spring. Therefore, apart from loss during the physical transport by water masses, higher fish predation pressure may explain the absence or scarcity of *Euchaeta* in Tolo Harbour. *E. concinna* performs diel vertical migration and diel feeding rhythm in Mirs Bay, suggesting it is susceptible to visual predators in shallow coastal areas.

Euchaeta concinna females feed predominantly on other small copepods (> 40%) in the field. Small copepods including *Acrocalanus*, *Paracalanus* and *Parvocalanus* are the preferred prey. Larger copepods such as copepodids of *Canthocalanus* are not preferred. Adult females of *E. concinna* impose almost similar daily predation impact on *Acrocalanus* and *Paracalanus/Parvocalanus*. About 4.3% of the population is removed daily. As predation rates by copepodids are not determined in this study, predation by the entire population of *E. concinna* may be important in regulating the populations of small copepods as the number of copepodids C4 and C5 are often over 10-fold higher than that of adults. The predation impact of female *E. concinna*

estimated in the present study is compared to those of other carnivorous copepods and chaetognaths, and it is concluded that *Euchaeta* may play a significant role, at least during the peak seasons, in controlling the populations of other small copepods.

摘要

捕食性橈足類 *Euchaeta* 屬廣泛分佈于全球大部份熱帶及亞熱帶水域。在香港及南中國沿岸水域，此屬包含了某幾種最豐富及最大型的橈足類。我的論文研究調查了 *Euchaeta* 在香港東面沿岸水域的兩個水灣的地理分佈，晝夜垂直遷移及其對其他浮游生物捕食的影響。我們發現了三種 *Euchaeta* 出沒于研究範圍內。以數目計算，優勢種 *E. concinna* 佔所有 *Euchaeta* 的橈足類群落多于 70%以上，而 *E. rimana* 及 *E. plana* 則比較少見。所有三種 *Euchaeta* 皆有明顯的季節性分佈，牠們的繁盛時期秖于冬季及/或夏季出現。我們在 *Euchaeta* 群落中並沒有發現清楚的幼體發展模式，這反映出這三種 *Euchaeta* 並不是本地原生種，而是經由海洋水流從鄰近水域進入本港水域。成年及幼年 *Euchaeta* 的分佈局限于大鵬灣內。吐露港是多種重要商業價值海魚在冬季及初春的重要孕育地。因此，除了因水流輸送而流失外，大量的海魚捕食也解釋了 *Euchaeta* 在吐露港缺少及稀有的原因。我們發現 *E. concinna* 在大鵬灣內進行晝夜垂直遷移及晝夜進食，暗示這種大型橈足類在沿岸淺海水域備受依靠視覺獵食的捕食者的威脅。

我們的研究發現雌性的 *Euchaeta concinna* 在野外主要進食其他小型的橈足類(> 40%)。小型的橈足類包括 *Acrocalanus* 屬、*Paracalanus* 屬及 *Parvocalanus* 屬是 *E. concinna* 的首要獵物。比較大型的橈足類例如 *Canthocalanus* 屬的幼體則

是次要獵物。成年雌性 *E. concinna* 對 *Acrocalanus* 及 *Paracalanus/Parvocalanus* 的日常捕食影響幾乎近同，每天大約 4.3%的群落會因被獵食而流失。這個研究並沒有估計幼體的捕食率，但由於幼體 C4 及 C5 的數量通常多于成年 *E. concinna* 十倍以上，整體 *E. concinna* 群落的捕食或許會對其他小型橈足類群落作出重要的調整作用。我們以本研究所估計出的雌性 *E. concinna* 捕食影響與其他食肉性橈足類及毛顎類作比較，得出結論 *Euchaeta* 至少在其數量繁多的季節可能對調整其他小型橈足類群落扮演著重要的地位。

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CHAPTER 1 GENERAL INTRODUCTION

1.1 Copepod and its ecological importance

Copepods are common in marine environments ranging from estuaries to open oceans. In the marine plankton, copepods are usually the dominant component of the zooplankton assemblages in terms of numerical abundance and play an important role in the function of the food web. Herbivorous copepods, the most important primary consumers in the marine plankton, form the base of virtually all pelagic food webs. Omnivorous or carnivorous copepods feed on other small zooplankton and impose structuring forces on the population size and composition of the prey assemblages (Sommer *et al.* 2003; Stibor *et al.* 2004). Planktonic copepods are the principal food items for many planktivorous fishes. Therefore, knowledge on population dynamics of planktonic copepods serves as the basis for both marine ecology and fishery management.

1.2 General biology of copepod

Most copepods are small in size, with body length ranging from about one mm

long to more than 10 mm long. Copepods come in different body shapes: elongated, fusiform or cylindrical, but all consist of 16 somites. The first six are generally fused into a cephalosome and the remaining 10 form the metasome and urosome (Fig. 1.1). In general, copepods have 12 pairs of appendages for swimming and feeding: the first and second antennae, mandibles, first and second maxillae, maxillipeds, five pairs of swimming legs (sometimes with the fifth legs modified as copulatory organs in male) and the reduced leg-like structures or sixth legs. The form of each pair of the appendages is variably modified in different copepod species.

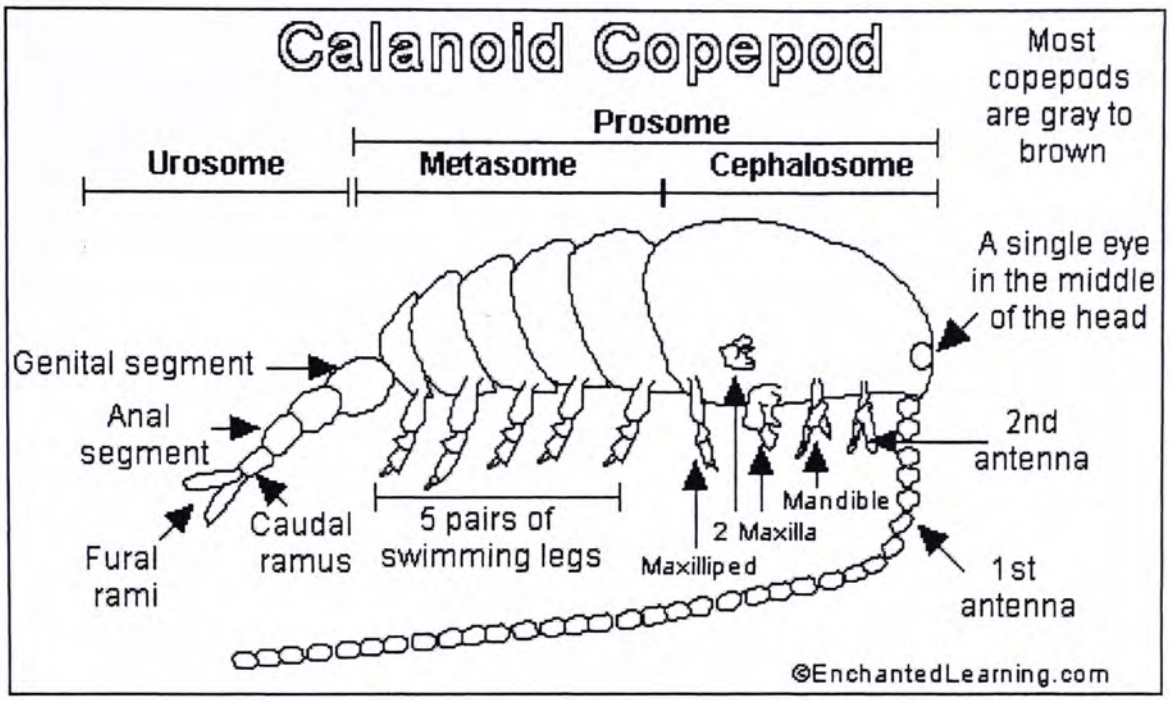

Figure 1.1 Diagram of a calanoid copepod (from http://www.enchantedlearning.com).

The development of copepods involves a series of anamorphic metamorphosis, which refers to a successive addition of somites and appendages at each moulting process. Copulation of copepod takes place when the male attaches a spermatophore, which is filled with sperms and other secretion, into the genital field of the female. Directly upon the fertilization, the fertilized eggs pass into the water or into an egg sac. The duration of the embryonic development depends on numerous factors, one of the most important being the temperature. When it is completed, the egg sac is released by the female into water and the eggs hatch into larva called nauplius. The naupliar larva involve six naupliar stage (from N1 to N6), in which five moulting process is carried out for development in body form including segmentation, size, structure of antennae, mandibles, other oral appendages and the first pair of legs. After N6, the larva moult into adult-like juvenile stage called copepodid which is accompanied with significant morphological change. Followed by another five moults (C1 to C5), development of the remaining pair of legs and sex differentiation are completed and the copepodids (C5) develop into the sexually mature adults. In general, each copepodid stage is identified by the number of segment and pairs of swimming leg formed (Fig. 1.2).

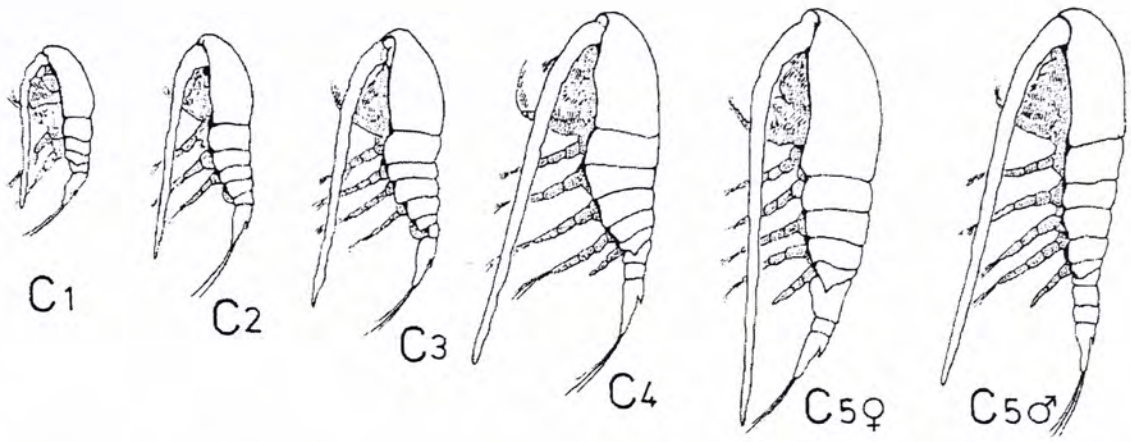

Figure 1.2 Development of a calanoid copepod from coppeodid stage C1 to C5. (Extracted from Dussart and Defaye, 1995). For *Euchaeta* spp., number of prosome segment: C1 – 3 segments; C2, C3, C4 and C5 – 4 segments. Number of urosome segment: C1, C2 and C3 – 2 segments; C4 – 3 segments; C5 – 4 segments. Pair of swimming legs: C1 – 2 pairs; C2 – 3 pairs; C3 – 4 pairs; C4 and C5 – 4 pairs (female) or 5 pairs (male).

1.3 Hydrography of Hong Kong

Hong Kong, located at the southern coast of China, is influenced by the South China Sea and connected with the East China Sea through the Taiwan Strait. The marine environment is affected by several water masses from different sources. To the west, freshwater discharged from the Pearl River reduces surface salinity, especially during the rainy season in spring and summer, and creates an estuarine environment of low salinity, uniform temperature and high sediment loading. In contrast, the southern and eastern waters of Hong Kong are characterized by oceanic waters of high salinity and are influenced seasonally by water masses from the South China Surface Current, the Kuroshio Current and the China Coastal Current (Morton and Morton 1983). During the northeast monsoon period in winter (December to March), southward movement of the China Coastal Current carries cold water masses from the East China Sea into the Taiwan Strait and Hong Kong. Meanwhile, warm waters from the Kuroshio Current enter into the South China Sea via the Luzon Strait. In spring (April and May), relaxation of the northeast monsoon and the China Coastal Current allows the Kuroshio Current to intrude further into the southern coast of China. In summer (June to September), the southwest monsoon prevails and the South China Sea Surface Current moves northward, carrying warm water masses from the South China Sea into

the coastal areas of southern China. This complex pattern of water circulation exerts a strong influence on the seasonal occurrence of copepod assemblages in Chinese coastal waters (Hwang and Wong 2005). The copepod communities in coastal seas around Hong Kong include species from both the East China Sea and the South China Sea (Zhang and Wong in prep.).

1.4 Copepods in Hong Kong's waters

The copepod communities in Hong Kong's coastal waters are characterized by warm-water coastal species (Chen 1982; Wong *et al.* 1993) on which little is known when compared with oceanic species. A preliminary study conducted by Chen (1982) in the coastal waters in Hong Kong includes a total of 52 species of Copepoda. Paracalanidae, Calanidae, Eucalanidae, Acartiidae, Temoridae, Euchaetidae, Pontellidae, Oithonidae and Corycaeidae are the most common copepod families recorded. Species diversity of copepods is higher in oceanic waters to the south and east of Hong Kong than in the estuarine waters of western Hong Kong.

Copepod communities in the coastal waters of Hong Kong exhibit pronounced spatial variations in species composition (Tam 1998; Lee 2003; Chen *et al.* 2003).

Estuarine waters to the west of Hong Kong are characterized by a preponderance of brackish-water species such as *Pseudodiaptomus poplesia* and *Acartiella sinensis*, especially in summer. Stenohaline copepod such as *Paracalanus parvus* is mostly restricted to the southeastern part of Hong Kong, while species such as *Parvocalanus crassirotris* is abundant in both the west and the east. Information on the composition and distribution of copepods in the eastern part of Hong Kong, especially in offshore areas outside Tolo Harbour is relatively limited. Wong *et al.* (1993) described 23 species of calanoid copepods in Tolo Harbour and identified copepods as the most important component of the coastal zooplankton in terms of species diversity. Copepod assemblages in Tolo Harbour are dominated by small copepods of the genera *Paracalanus* and *Oithona*.

Little is known about the feeding ecology and trophic role of copepods in the Chinese coast. Most of the feeding studies on copepods in Chinese waters focused on the grazing activities of herbivorous species (Yang 1997; Hwang *et al.* 1998; Wang *et al.* 1998; Li and Wang 2000, 2003; Li *et al.* 2002a, 2002b, 2004), probably due to their high abundance in inshore waters, especially in small eutrophic bays. Despite its ecological importance, predatory copepods in the coastal waters of Hong Kong and southern China have not received much attention and the trophic interactions at the

grazer-predator level in tropical and subtropical seas are poorly known. The family Euchaetidae is widespread in the world and consists of the genera *Euchaeta* and *Pareuchaeta* (Park 1995). Park (1995) recognized 14 species of *Euchaeta* and 61 species of *Pareuchaeta*. Eight species of *Euchaeta* have been recorded in Chinese seas including the South China Sea, the East China Sea, the Yellow Sea and the Taiwan Strait (Chen and Zhang 1965; Chen and Shen 1974; Zheng *et al.* 1985). In comparison, only one species of *Pareuchaeta* has been recorded in Chinese waters (Lo *et al.* 2004). Four species of *Euchaeta* including *E. concinna*, *E. indica*, *E. plana* and *E. rimana* have been recorded in seas around Hong Kong in previous studies (Chen 1982; Chan 1995; Chen *et al.* 2003; Lee 2003).

Species belonging to the family Euchaetidae (Fig. 1.3) are generally large in size (2–12 mm), strictly carnivorous and widely distributed. *Pareuchaeta* has been extensively studied in temperate and arctic regions (Yen 1991; Øresland 1991, 1995; Mauchline 1995; Alonzo *et al.* 2000; Fleddum *et al.* 2001; Skarra and Kaartvedt 2003) and is considered to play an important role in the pelagic food chains because of its feeding behaviour (Båmstedt and Skjoldal 1976; Bakke 1977; Bathmann *et al.* 1990; Eiane *et al.* 2002). In comparison, information on the tropical and subtropical genus *Euchaeta* is very limited, and in view of its abundance and wide distribution in

Chinese waters, there is a need to study its distribution and feeding ecology.

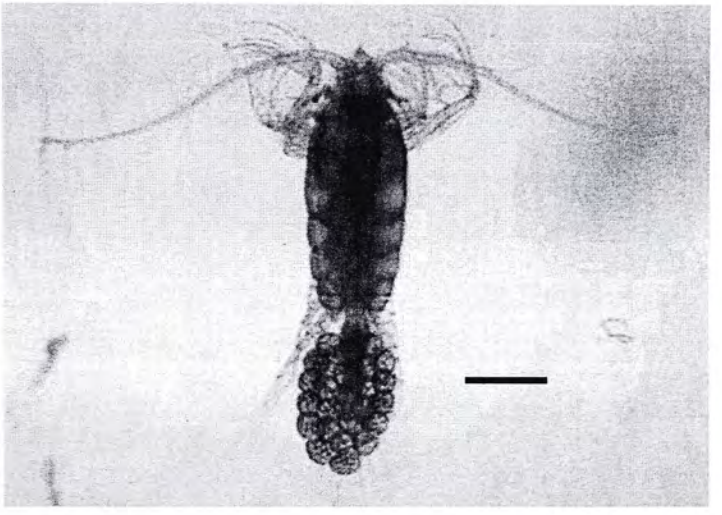

Figure 1.3 Adult female of *Euchaeta concinna* with egg sac. Bar = 1 mm.

1.5 Diel vertical migration (DVM)

Diel vertical migration (DVM) by zooplankton affects the trophodynamics of local marine ecosystems as animals performing DVM change their vertical distribution in the water column on a 24-h cycle and consequently feeding at different times of the day and in different depth strata. The normal pattern of DVM is for the population to stay in the deeper layers during daytime to avoid visual predators and perhaps to gain metabolic advantages, and rise to the surface for a few hours at night to feed (Gabriel and Thomas 1988; Longhurst and Harrison 1989). DVM is a phenotypically flexible behaviour whose pattern can be influenced by various external and internal factors (Forward *et al.* 1984; Ohman 1990; Bollens and Frost 1991a; Vestheim *et al.* 2005). Large copepods are susceptible to predation by visual predators and DVM may be essential where fish predation pressure is high. DVM by *Pareuchaeta* has been studied in the temperate waters. *Pareuchaeta elongate* in Dabob Bay of Washington performs normal DVM (Bollens and Frost 1991a), while *P. norvegica* in the Norwegian fjords exhibits a bimodel DVM pattern in which only populations in the upper layers migrate while individuals with fat reserve remain in the bottom layers at night (Kaartvedt *et al.* 2002; Vestheim *et al.* 2005). Information on the diel vertical distribution of *Euchaeta* in tropical and subtropical regions is scarce

and tends to consist of qualitative descriptions (Chen *et al.* 1980; Yang *et al.* 1999a, 1999b).

1.6 Thesis content

This study aims to provide information on the ecology of one of the largest and most common predatory copepods in the eastern coastal waters of Hong Kong. The research consists of (1) a study on the seasonal distribution and population dynamics of *Euchaeta*, and (2) a study on the diel vertical distribution and feeding activities of *Euchaeta concinna*, the most common Euchaetidae in Mirs Bay.

CHAPTER 2 DISTRIBUTION AND POPULATION DYNAMICS OF *EUCHAETA* SPEICES IN THE COASTAL WATERS OF EASTERN HONG KONG

2.1 Introduction

2.1.1 Diversity of *Euchaeta* along the Chinese waters

The genus *Euchaeta* is widely distributed in subtropical and tropical oceans (Park 1995) and represents one of the most abundant and largest predatory copepods in the coastal waters of Hong Kong and southern China (Chen 1982; Hwang *et al.* 2003; Lee and Chen 2003; Yang *et al.* 2004). A total of eight species of *Euchaeta* has been recorded in seas along the Chinese coast (Table 2.1). *Euchaeta concinna*, *E. indica*, *E. longicornis*, *E. plana* and *E. rimana* have been found in the East China Sea, while *E. concinna*, *E. plana* and *E. rimana* have been reported from the Yellow Sea (Chen and Zhang, 1965). Seven species were recorded in the South China Sea, including *E. media* and *E. spinosa* as well as the five species found in the East China Sea and Yellow Sea (Chen and Shen 1974). Four (*E. concinna*, *E. indica*, *E. plana* and *E. rimana*) of the seven species reported in the South China Sea have reached the

Table 2.1 Occurrence (√) of *Euchaeta* spp. in Chinese waters according to Chen and Zhang 1965 (1), Chen and Shen 1974 (2), Chen 1982 (3), Zheng *et al.* 1985 (4), Chan 1995 (5), Chen *et al.* 2003 (6), Hwang *et al.* 2003 (7), Lee 2003 (8), Lo *et al.* 2004 (9), Yang *et al.* 2004 (10), and this study. ++ represents dominant species.

Species	Hong Kong				Taiwan			Mainland China		
	Offshore eastern waters	Inshore eastern waters	Southern waters	Western waters	Taiwan Strait	Southern waters	Northern waters	South China Sea	East China Sea	Yellow Sea
	This study	3	3, 5, 8	6	4, 10	7	9	2, 4	1, 4	1, 4
Euchaeta acuta Giesbrecht, 1892							√			
Euchaeta concinna Dana, 1849	++	√	++	++	√	√	√	√	√	√
Euchaeta indica Wolfenden, 1905			√	√	√			√	√	
Euchaeta longicornis Giesbrecht, 1888							√	√	√	
Euchaeta media Giesbrecht, 1888							√	√		
Euchaeta plana Mori, 1937	√		√	√	√			√	√	√
Euchaeta rimana Bradford, 1974	√	√	√		√	√	√	√	√	√
Euchaeta spinosa Giesbrecht, 1892								√		

Taiwan Strait (Zheng *et al.* 1985; Yang *et al.* 2004). Hwang *et al.* (2003) collected zooplankton samples in southern Taiwan and only found two species (*E. concinna* and *E. rimana*). In contrast, Lo *et al.* (2004) reported a more diverse community consisting of five species in northern Taiwan, including *E. acuta*, *E. concinna*, *E. longicornis*, *E. media* and *E. rimana* as well as *E. acuta* which has not been recorded in the Chinese coast previously.

In Hong Kong, four species of *Euchaeta*, including *E. concinna*, *E. indica*, *E. plana* and *E. rimana*, have been reported (Table 2.1). *E. concinna*, the most common species, occurs in western, southern and eastern waters. With the exception of *E. plana* which can be found in seas all around Hong Kong, the other two species tend to occur only in parts of Hong Kong (Chen 1982; Chen *et al.* 2003; Chan 1995; Lee 2003). All four species are widely distributed along the Chinese coast from the South China Sea in the south to the Yellow Sea in the north (Chen and Zhang 1965; Chen and Shen 1974; Zheng *et al.* 1985; Hwang *et al.* 2003; Lo *et al.* 2004; Yang *et al.* 2004). Park (1995) described the four species recorded in Hong Kong as Indo-Pacific in distribution. *E. concinna* was first described from the tropical Pacific and has since been found often in large numbers in the Malay Archipelago, the Indian Ocean, the Bay of Bengal, the Arabian Sea, the Great Barrier Reef, the Pacific coast of central

Japan, and the western equatorial Pacific. The range of *E. rimana* extends over tropical, subtrophical and temperate regions in the Pacific and Indian Oceans. *Euchaeta plana* has been described from the East China Sea, the Izu region of Japan, southern and central Japan, the Arabian Sea and the Malay Archipelago. *Euchaeta indica* has been found in tropical waters of the Pacific Ocean from the American coast to the Malay Archipelago, subtropical water of the eastern Indian Ocean and temperate waters off southern Japan.

2.1.2 Seasonal occurrence of *Euchaeta*

Euchaeta species show strong seasonality of occurrence in the coastal waters of Hong Kong. Peak densities are usually recorded in winter and spring when the northeast monsoon prevails (Chen 1982; Chen *et al.* 2003; Lee 2003). Chen *et al.* (2003) reported that *E. concinna* is rare in the Pearl River Estuary during summer and autumn, but becomes more abundant during winter and spring. Similarly, *E. indica* is found in the southeastern water of Hong Kong only during winter and spring (Lee 2003). Lee and Chen (2003) reported that northern boreal copepods such as *E. plana* are carried into Hong Kong coastal waters in winter by the China Coastal Current. These authors further suggested that copepod species composition and abundance in

local waters are affected by seasonal changes in water circulation and intrusion of water masses with distinctive species assemblages. Similar pattern of seasonal occurrence is also reported in the southwestern waters of Taiwan for *E. concinna* and *E. rimana* which reach peak densities in January and become rare in June and October (Hwang *et al.* 2003).

Seasonal occurrence of *Euchaeta* species in the East China Sea and the Yellow Sea is different from that observed in southern China. *Euchaeta concinna*, *E. rimana* and *E. plana* become numerically abundant in summer and autumn in the East China Sea and the southern part of the Yellow Sea (Chen and Zhang, 1965). Chen and Zhang (1965) further noted that the copepod communities in these waters are dominated by tropical and subtropical species including *E. concinna*, *E. rimana* and *E. plana* in summer and autumn when water masses from offshore waters of the East China Sea are moved northwest towards central East China Sea and the Yellow Sea by winds blowing from the southeast. Similar observation was made by Cheng (1965) who reported that the densities of *E. concinna* and *E. plana* in the Yellow Sea and the western East China Sea increase substantially in summer and autumn. The author further explained the seasonal changes of copepod community in these regions in relation to changes in hydrographic conditions, in particular, seasonal changes in the

movement of water masses and currents. The predominance of tropical species including *E. concinna* and *E. plana* in summer and autumn is explained by the intrusion of warm and saline water from offshore areas into the coastal waters under the influence of Kuroshio Current. The coastal environment of northern Taiwan is influenced by both the China Coastal Current and the Kuroshio Current in various seasons and *Euchaeta* species including *E. concinna*, *E. rimana* and *E. plana* occur throughout the year but become most abundant in autumn and winter (Yang *et al.* 1999a). In winter, *E. rimana* becomes the dominant species, comprising 67% of total copepod population and reaching densities of 40.2 ind.m^{-3} (Yang *et al.* 1999b).

2.1.3 Study area

The hydrology of the coastal waters of Hong Kong has been described in chapter 1. Tolo Harbour and Mirs Bay, located in the northeastern part of Hong Kong, cover most of the eastern waters (Fig. 2.1). Tolo Harbour is an almost enclosed bay with an average depth of about 10 m and a maximum depth of 22 m. It opens into Mirs Bay, a much bigger inlet which is fully exposed to the water currents from the South China Sea. Due to its semi-enclosed topography, poor tidal exchange and a long history of eutrophication, the marine environment of Tolo Harbour is characterized by high

phytoplankton biomass and frequent algal blooms (Morton 1989). Wong *et al.* (1993) provides the only study on the species composition of the zooplankton community in Tolo Harbour. Small copepods (body size < 1 mm) such as *Parvocalanus crassirostris*, *Paracalanus parvus, Oithona rigida* and *O. simplex* are common, while large copepods (> 2 mm) such as *Euchaeta* spp. are extremely rare. In comparison, copepod species composition in Mirs Bay, especially the offshore areas, is poorly known. According to Chen (1982), *E. concinna* and *E. rimana* can be found in the near-shore areas of Mirs Bay.

It is hypothesized that *Euchaeta* species are transported into the coastal areas around Hong Kong by the water masses from the neighbouring Chinese Seas. Based on this hypothesis, the occurrence of *Euchaeta* species should be related to seasonal changes in water circulation. In addition, the diversity and abundance of *Euchaeta* should be lower in Tolo Harbour than in Mirs Bay.

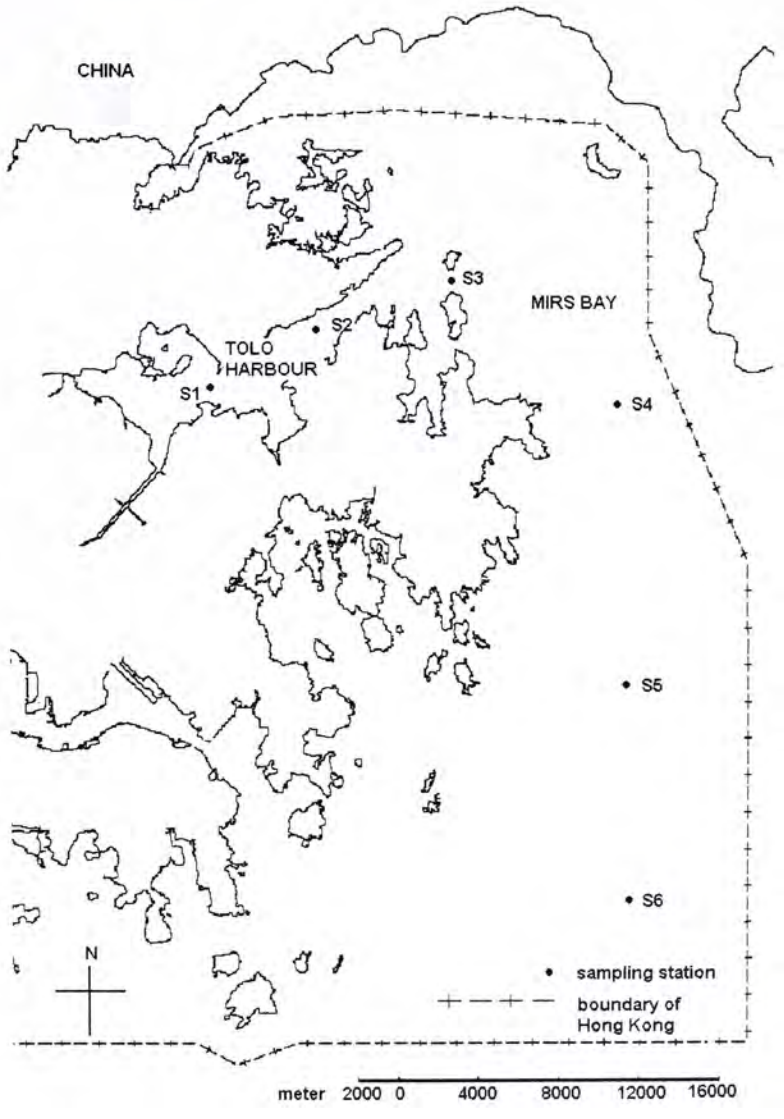

Figure 2.1 Map of Hong Kong showing the sampling stations in Tolo Harbour (S1 and S2) and Mirs Bay (S3, S4, S5 and S6).

2.1.4 Objectives of study

This study aims to: (1) study the species composition of *Euchaeta* in the coastal waters of eastern Hong Kong which is fully exposed to ocean currents from the South China Sea, (2) study the seasonal occurrences of *Euchaeta* in the eastern parts in relation to hydrographic factors including water temperature and salinity, and (3) compare the spatial distribution of *Euchaeta* between Tolo Harbour and Mirs Bay.

2.2 Materials and Methods

2.2.1 Field sampling

Field sampling was conducted at intervals of two to three weeks at six sampling stations over a two-year period from July 2003 to June 2005 (Fig. 2.1). Two stations (S1 and S2) were located in Tolo Harbour and four stations (S3, S4, S5 and S6) were located in Mirs Bay. Station locations were fixed with a GPS device and water depth at each station is shown in Table 2.2. Duplicated zooplankton samples were collected at each station by making vertical hauls from 2 m above the bottom to the surface with a plankton net (50 cm mouth diameter, 125 μm mesh size). Collected samples were immediately preserved in 4% buffered formaldehyde-seawater solution. All samples were collected between 1000 h and 1600 h to minimize diurnal variations in zooplankton abundance.

Temperature and salinity were measured at the surface (0.5 m) of each station at the time of zooplankton sampling. The vertical profiles of water temperature, salinity, dissolved oxygen (DO) and light intensity were also obtained at S1 in Tolo Harbour and S6 in Mirs Bay (S6) once in every season (spring, summer, autumn and

Table 2.2 Locations and water depths (mean and range) of sampling stations in Tolo Harbour (S1 and S2) and Mirs Bay (S3, S4, S5 and S6).

Sampling station	Coordinates		Water depth (m)
S1	22° 26.725'N	114° 14.566'E	14 (10–16)
S2	22° 28.539'N	114° 18.034'E	20 (18–23)
S3	22° 29.468'N	114° 21.588'E	21 (20–25)
S4	22° 26.670'N	114° 26.920'E	21 (20–26)
S5	22° 17.560'N	114° 26.920'E	26 (24–29)
S6	22° 13.000'N	114° 26.920'E	30 (28–33)

winter). Water temperature, salinity and dissolved oxygen (DO) were measured with a Hydrolab H20 water analysis system. Light intensity was measured with a light meter and expressed as light refractive index which represents the ratio of light intensity measured in water to light intensity measured in the air.

2.2.2 Laboratory analysis

In the laboratory, zooplankton samples were examined under a stereomicroscope and the density of *Euchaeta* species was determined by counting entire samples. One of the most important morphological characters for taxonomic identification of *Euchaeta* is the structure of the reproductive organs. Adult *Euchaeta* specimen was identified to species according to the descriptions of Park (1995). Copepodids (C1, C2, C3, C4 and C5) were only identified to the genus level due to the absence or incomplete development of the reproductive structures.

2.2.3 Data analysis

Data collected from replicate samples was presented as mean value with standard deviation (SD). Differences between samples were tested using ANOVA.

Nonparametric ANOVA was used if assumptions of normality (Normality Test) or homogeneity of variance (Equal Variance Test) were not met. To compare results between seasons (spring : April and May; summer: June, July, August and September; autumn: October and November; winter: December, January, February and March), pooled data collected from different months were tested. In all cases, the alpha level was 0.05. All statistical tests were conducted using software SigmaStat 3.1 and statistical results on ANOVA (or nonparametric ANOVA) are included in the Appendices.

2.3 Results

2.3.1 Hydrography

Surface water temperature in the study area was higher in summer and lower in winter (Fig. 2.2). The lowest temperature of about 15°C occurred between January and February, while the highest temperature of 30°C occurred between July and September. Surface water temperature was significantly higher in summer (June, July, August and September) than in winter (December, January, February and March) (Kruskal-Wallis One Way ANOVA on Ranks, $P < 0.001$), but did not differ significantly among sampling stations (Kruskal-Wallis One Way ANOVA on Ranks, $P = 0.618$).

Surface salinity at the six sampling stations ranged from 22 to 37 (Fig. 2.2). Variations in salinity reflected seasonal patterns in precipitation. Salinity was significantly lower in spring (April and May) and summer (June, July, August and September) than in autumn (October and November) and winter (December, January, February and March) (One-way ANOVA, $P < 0.001$). Over the entire study period, surface salinity did not differ significantly among sampling stations (Kruskal-Wallis

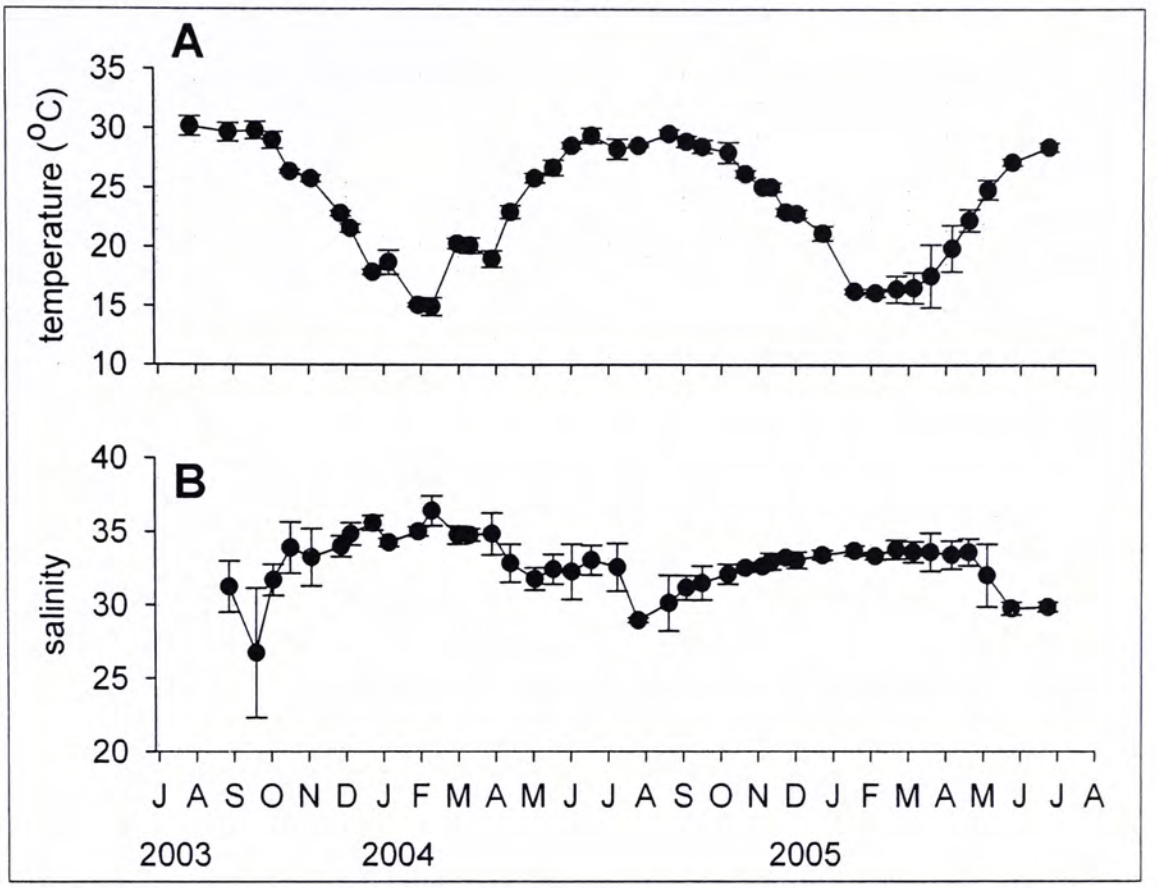

Figure 2.2 Seasonal variations in surface water temperature (A) and salinity (B). Each point represents the mean (± SD) of six sampling stations.

One Way ANOVA on Ranks, $P = 0.179$).

Vertical variations in water temperature, salinity and DO in Tolo Harbour (S1) and Mirs Bay (S6) were studied in different seasons. No vertical stratification of the water columns was observed in Tolo Harbour in autumn and winter (Fig. 2.3). Water temperature, salinity and DO did not vary with depth, indicating that the water column was fully mixed. However, vertical stratification of water column was observed in Tolo Harbour during spring and summer. Water temperature and DO tended to be highest at the surface, decreased with increasing depth, and became relatively constant between 8 m and the bottom. In spring and summer, salinity was lowest at the surface and increased with depth. Anoxia of the bottom layer was observed in summer when seawater below 8 m contained < 1 mg O_2 L^{-1}. In contrast, water temperature, DO and salinity remained relatively constant along the water column in Mirs Bay (S6) throughout the year due to strong mixing by water currents from the open ocean (Fig. 2.4).

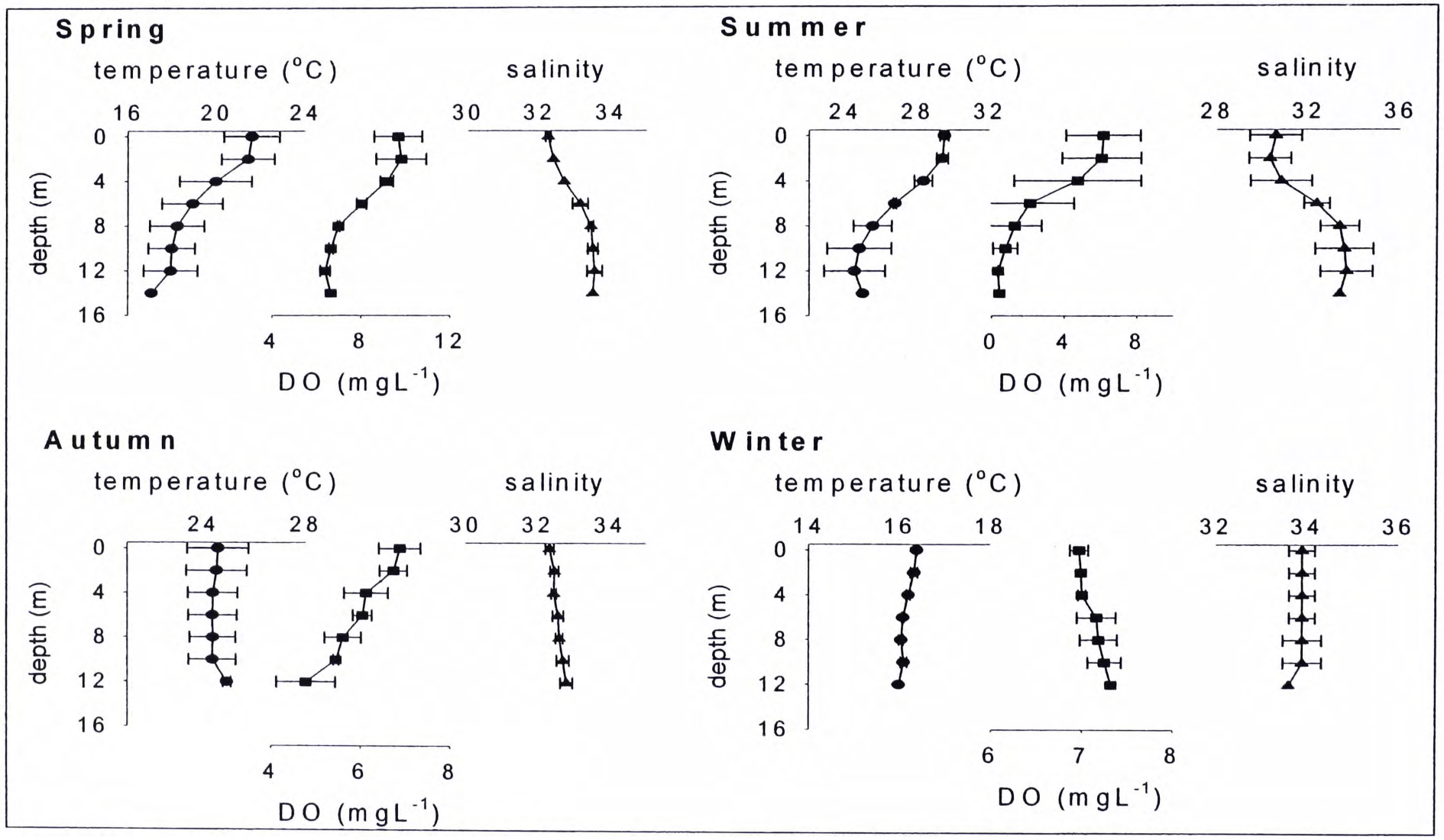

Figure 2.3 Vertical profiles of mean (± SD) water temperature (●), salinity (▲) and DO (■) at S1 in Tolo Harbour. (Spring = Apr and May; Summer = June, July, August and September; Autumn = October and November; Winter = December, January, February and March).

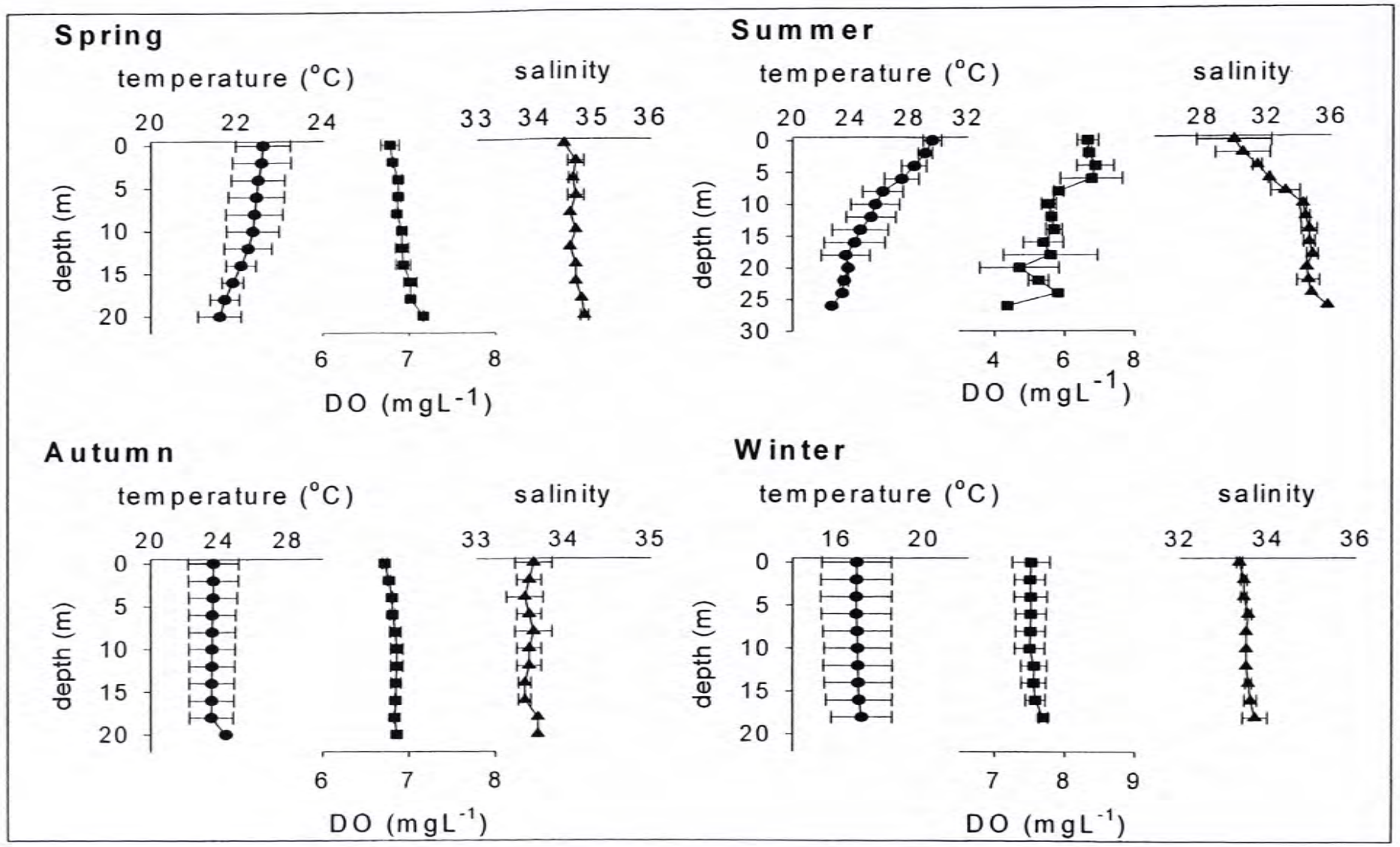

Figure 2.4 Vertical profiles of mean (± SD) water temperature (●), salinity (▲) and DO (■) at S6 in Mirs Bay. (Spring = Apr and May; Summer = June, July, August and September; Autumn = October and November; Winter = December, January, February and March).

Water in the semi-enclosed Tolo Harbour was less transparent due to higher amount of suspended particles and higher phytoplankton biomass. Light reflective index at the surface was lower in Tolo Harbour (S1) than in Mirs Bay (S6) (Fig. 2.5). In Tolo Harbour, light intensity was reduced by more than 90% (light refractive index < 0.1) at 10 m while a similar reduction in light intensity occurred at 15 m in Mirs Bay.

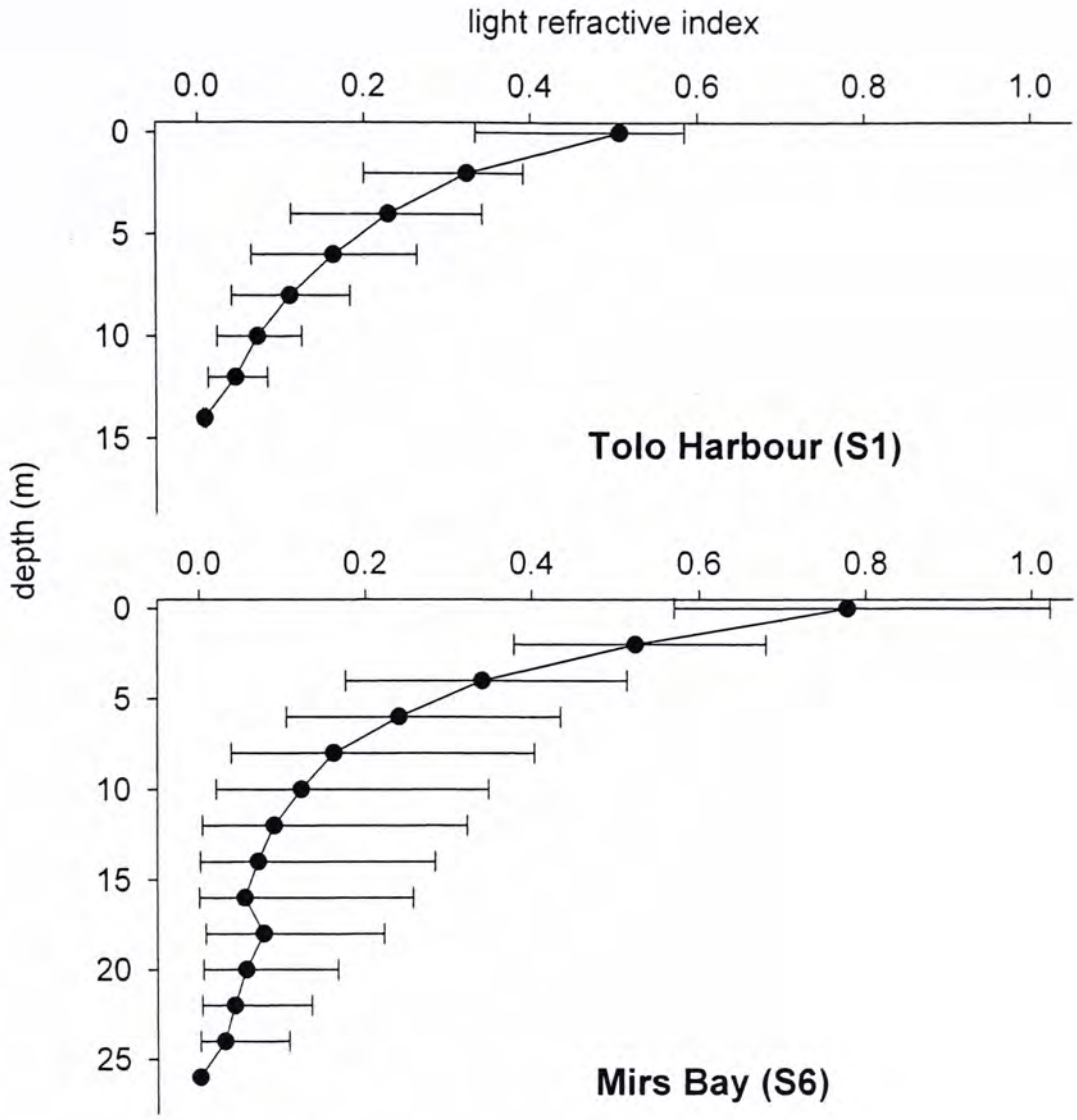

Figure 2.5 Vertical profiles of light refractive index at S1 in Tolo Harbour and S6 in Mirs Bay. Each point represents the average (± SD) over the entire sampling period from July 2003 to June 2005. Light refractive index is the ratio of light intensity measured in water at each water depth to light intensity measured in the air.

2.3.2 Species diversity

Three species of *Euchaeta* (*E. concinna*, *E. rimana* and *E. plana*) were recorded in Tolo Harbour and Mirs Bay (Table 2.3). *Euchaeta concinna*, the most abundant species, comprised about 73% of the total population of *Euchaeta*. The two less abundant species, *E. rimana* and *E. plana*, comprised, respectively, 16% and 11% of the total population of *Euchaeta*. Over the entire study period, the average densities of *E. concinna*, *E. rimana* and *E. plana* at all sampling stations in the study area were 0.7, 0.2 and 0.1 ind.m^{-3}, respectively. For copepodids, the average densities of C1, C2, C3, C4 and C5 were 0.3, 0.6, 1.3, 1.2 and 1.4 ind.m^{-3} respectively (Table 2.4).

2.3.3 Spatial distribution

Euchaeta concinna and *E. plana* were found at all stations in Tolo Harbour (S1 and S2) and Mirs Bay (S3, S4, S5 and S6), while *E. rimana* was found only at S2, S3, S4, S5 and S6 (Table 2.3). All three species exhibited a clear seaward increase in abundance. Over the entire study period, *E. concinna* was rare at S1, S2 and S3 (mean abundance < 0.1–0.4 ind.m^{-3}) but became much more common at S4, S5 and S6 (1.0–1.2 ind.m^{-3}). *Euchaeta rimana* was absent at S1 but was relatively common at

Table 2.3. Density (mean and range) and relative abundance (mean and range) of three *Euchaeta* species at sampling stations in Tolo Harbour (S1 and S2) and Mirs Bay (S3, S4, S5 and S6). Each value represents the average over the entire study period from July 2003 to June 2005.

Species	Density (ind. m^{-3})							Relative abundance (%)
	S1	S2	S3	S4	S5	S6	Overall total	
E. concinna	<0.1 (0-6.3)	0.4 (0-9.8)	0.3 (0-2.8)	1.1 (0-19.4)	1.0 (0-17.3)	1.2 (0-12.3)	0.69 (0-19.4)	73.4 (0-87.4)
E. rimana	0 (0-0)	<0.1 (0-0)	<0.1 (0-0.1)	0.1 (0-1.1)	0.3 (0-6.5)	0.5 (0-5.4)	0.15 (0-6.5)	16.0 (0-24.0)
E. plana	<0.1 (0-0.2)	<0.1 (0-0.5)	<0.1 (0-0.2)	0.1 (0-1.7)	0.2 (0-3.3)	0.2 (0-1.8)	0.10 (0-3.3)	10.6 (0-12.2)
Total	<0.1 (0-6.5)	0.4 (0-10.3)	0.3 (0-3.1)	1.3 (0-22.2)	1.6 (0-27.1)	1.9 (0-19.5)	0.94 (0-27.1)	100

Table 2.4. Density (mean and range) and relative abundance (mean and range) of copepodids C1, C2, C3, C4 and C5 of *Euchaeta* at sampling stations in Tolo Harbur (S1 and S2) and Mirs Bay (S3, S4, S5 and S6). Each value represents the average over the entire study period from July 2003 to June 2005.

Copepodid stage	Density (ind. m^{-3})							Relative abundance (%)
	S1	S2	S3	S4	S5	S6	Overall total	
C1	0 (0-0)	<0.1 (0-0.9)	<0.1 (0-0.3)	0.7 (0-10.4)	1.0 (0-20.7)	0.3 (0-2.7)	0.3 (0-20.7)	6.3 (0-9.5)
C2	<0.1 (0-0.4)	0.1 (0-4.5)	0.1 (0-1.7)	0.6 (0-5.4)	2.1 (0-36.3)	0.8 (0-4.9)	0.6 (0-36.3)	12.5 (0-16.7)
C3	<0.1 (0-1.1)	0.4 (0-10.3)	0.5 (0-11.3)	1.2 (0-8.4)	4.1 (0-73.4)	1.7 (0-13.7)	1.3 (0-73.4)	27.1 (0-33.8)
C4	<0.1 (0-0.6)	0.5 (0-8.7)	0.5 (0-9.3)	1.8 (0-23.3)	2.7 (0-33.7)	2.0 (0-10.2)	1.2 (0-33.7)	25.0 (0-15.5)
C5	<0.1 (0-0.6)	0.4 (0-8.9)	0.4 (0-4.2)	2.2 (0-53.1)	2.8 (0-47.1)	2.3 (0-16.8)	1.4 (0-53.1)	29.2 (0-24.4)
Total	<0.1 (0-2.7)	1.4 (0-33.3)	1.5 (0-26.8)	6.5 (0-100.6)	12.7 (0-211.2)	7.1 (0-48.3)	4.8 (0-217.2)	100

S6 (0.5 ind.m^{-3}). *Euchaeta plana* was rare in the entire study area (< 0.1–0.2 ind.m^{-3}). Mean densities of all three species were significantly higher at S4, S5 and S6 than at S1, S2 and S3 (Kruskal-Wallis One Way ANOVA on Ranks, $P < 0.001$).

The spatial distribution of copepodids was similar to that of adults, exhibiting a clear trend of seaward increase in density. Copepodids were found at all sampling stations, although C1 was not recorded at S1 during the entire sampling period (Table. 2.4). In general, copepodids of all stages were rare at S1, S2 and S3 (< 0.1–1.5 ind.m^{-3}) but abundant at S4, S5 and S6 (6.5–12.7 ind.m^{-3}). For all copepodid stages, mean densities were significantly higher at S4, S5 and S6 than at S1, S2 and S3 (Kruskal-Wallis One Way ANOVA on Ranks, $P < 0.001$).

2.3.4 Seasonal occurrence

All three species of *Euchaeta* showed seasonal occurrence. In general, numbers were extremely low in summer (June, July, August and September) and autumn (October and November), but increased considerably in winter (December, January, February and March) and spring (April and May). Annually, *E. concinna* was most abundant in winter and spring and reached peak densities in December and January

(Fig. 2.6). Averaged over the entire study area, densities recorded in the winter were significantly higher than those recorded in other seasons (Kruskal-Wallis One Way ANOVA on Ranks, $P < 0.001$). *E. rimana* mainly appeared in the study area in April and May (Fig. 2.7). Densities in April and May were significantly higher than those in other months (Kruskal-Wallis One Way ANOVA on Ranks, both $P < 0.002$). *E. plana* occurred in the study area in winter and spring (Fig. 2.8). Densities in winter and spring were significantly higher than those in summer and autumn (Kruskal-Wallis One Way ANOVA on Ranks, both $P < 0.001$).

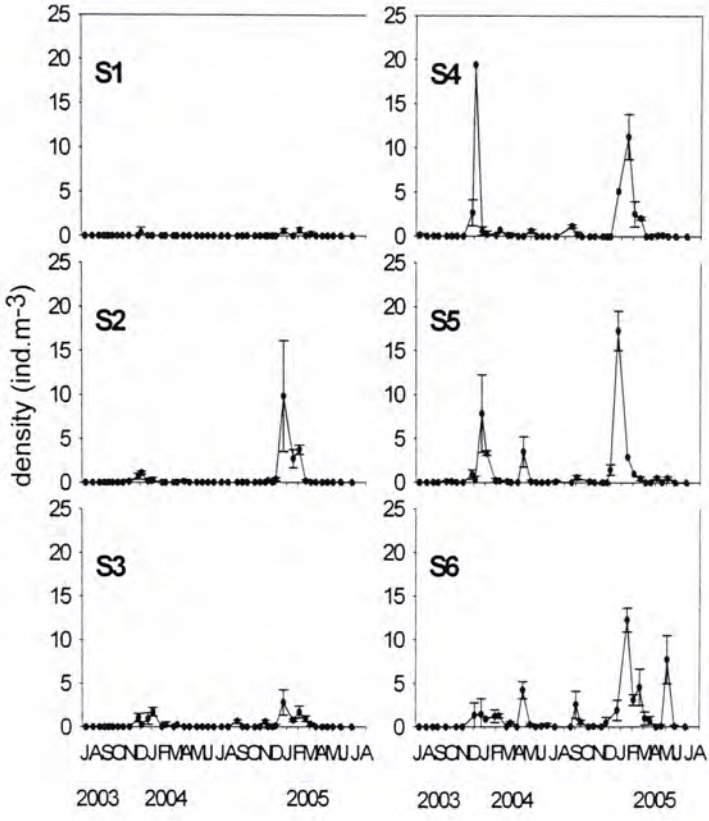

Figure 2.6. Monthly variations in the density (mean ± SD) of adult *Euchaeta concinna* at sampling stations in Tolo Harbour (S1 and S2) and Mirs Bay (S3, S4, S5 and S6).

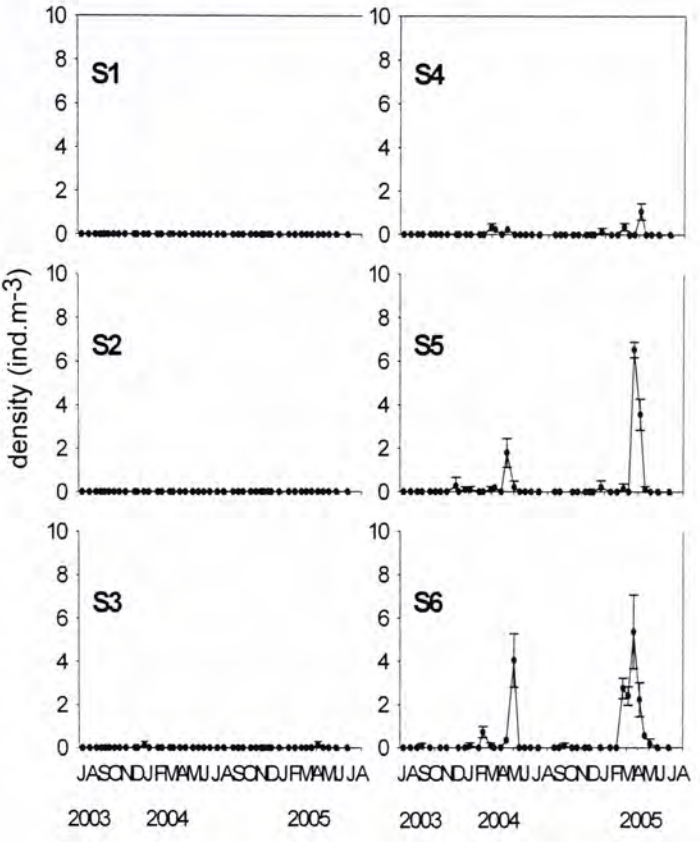

Figure 2.7. Monthly variations in the density (mean ± SD) of adult *Euchaeta rimana* at sampling stations in Tolo Harbour (S1 and S2) and Mirs Bay (S3, S4, S5 and S6).

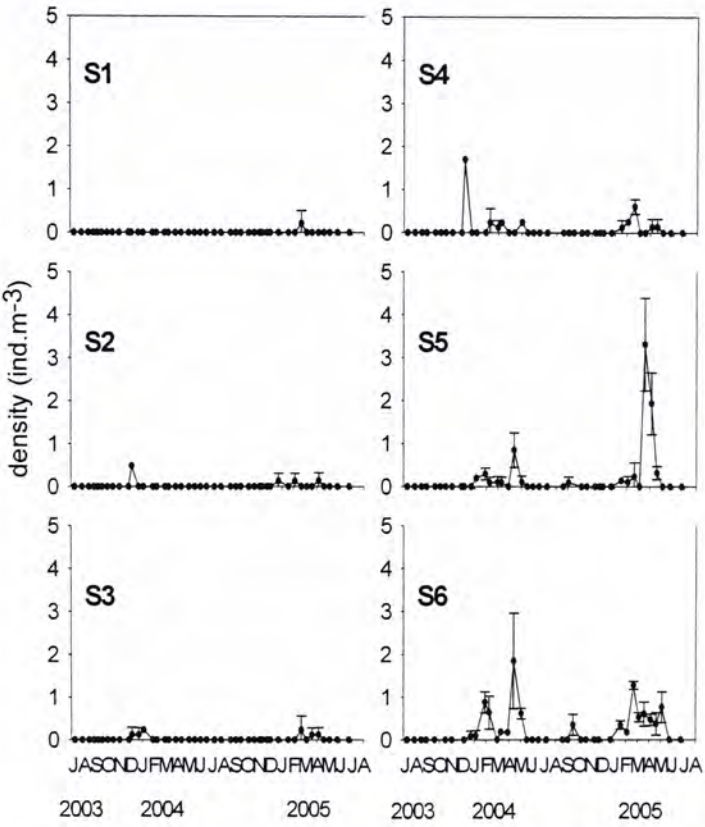

Figure 2.8. Monthly variations in the density (mean ± SD) of adult *Euchaeta plana* at sampling stations in Tolo Harbour (S1 and S2) and Mirs Bay (S3, S4, S5 and S6).

Occurrence of copepodids (C1, C2, C3, C4 and C5) was mostly restricted to winter and spring (Figure 2.9), although small number of copepodids could also be found during the summer and autumn. Copepodids of all stages became most abundant in early winter (December and January) and declined rapidly before the end of winter (March). For all copepodid stages, densities were significantly higher in winter than in the other seasons (Kruskal-Wallis One Way ANOVA on Ranks, all $P < 0.001$).

Occurrences of *Euchaeta concinna*, *E. rimana* and *E. plana* in relation to water temperature and salinity are showed in Figure 2.10. *Euchaeta* occurred in a wide range of temperature and salinity. In general, *E. concinna* was most abundant (density > 5 ind.m^{-3}) at water temperatures between 16 and 21°C. Compared with *E concinna, E. rimana* peaked (> 2 ind.m^{-3}) at slightly higher temperatures of 18 to 22°C. Peak densities of *E. plana* (> 1 ind.m^{-3}) were recorded at temperatures ranging from 16 to 22°C. All three species were common at salinities of 33 to 36. Copepodids were most abundant (> 5 ind.m^{-3}) in temperatures from 16 to 22 °C and salinities from 33 to 36 (Fig. 2.11). The abundance of adults and copepodids of all three species of *Euchaeta* correlated significantly and negatively with water temperature and significantly and positively with salinity (Table. 2.5).

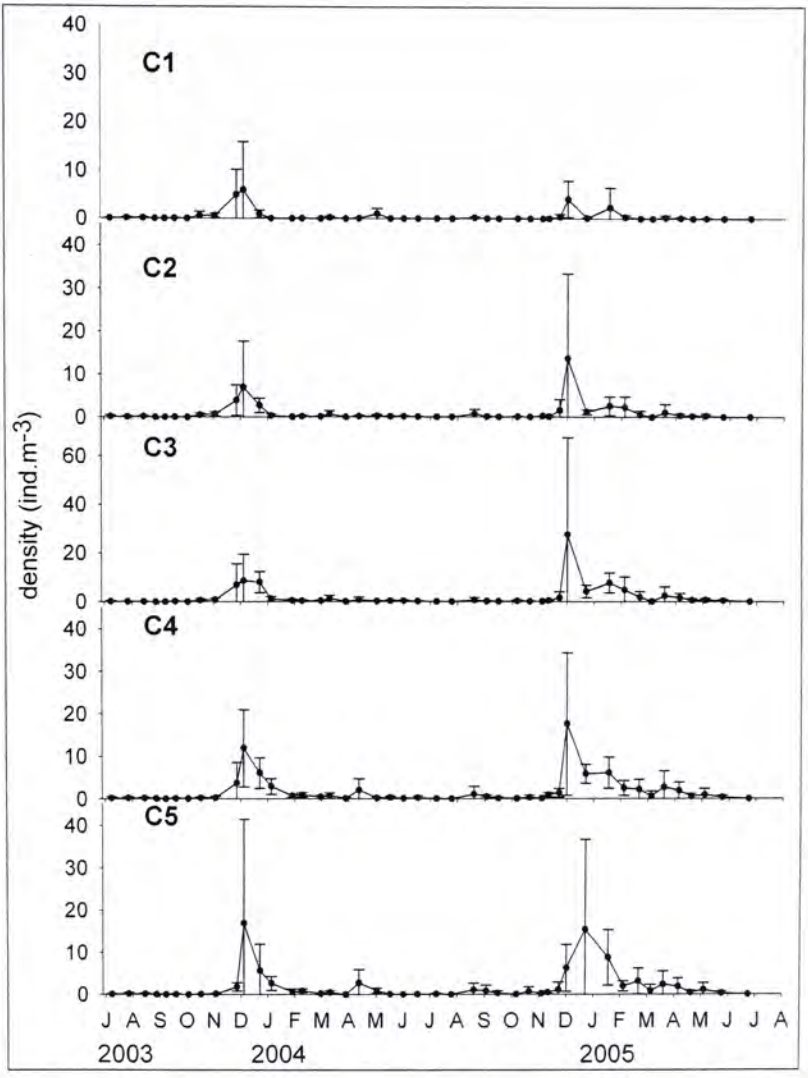

Figure 2.9. Monthly variations in the density (mean ± SD) of copepodids (C1, C2, C3, C4 and C5) of *Euchaeta* at sampling stations in Tolo Harbour (S1 and S2) and Mirs Bay (S3, S4, S5 and S6).

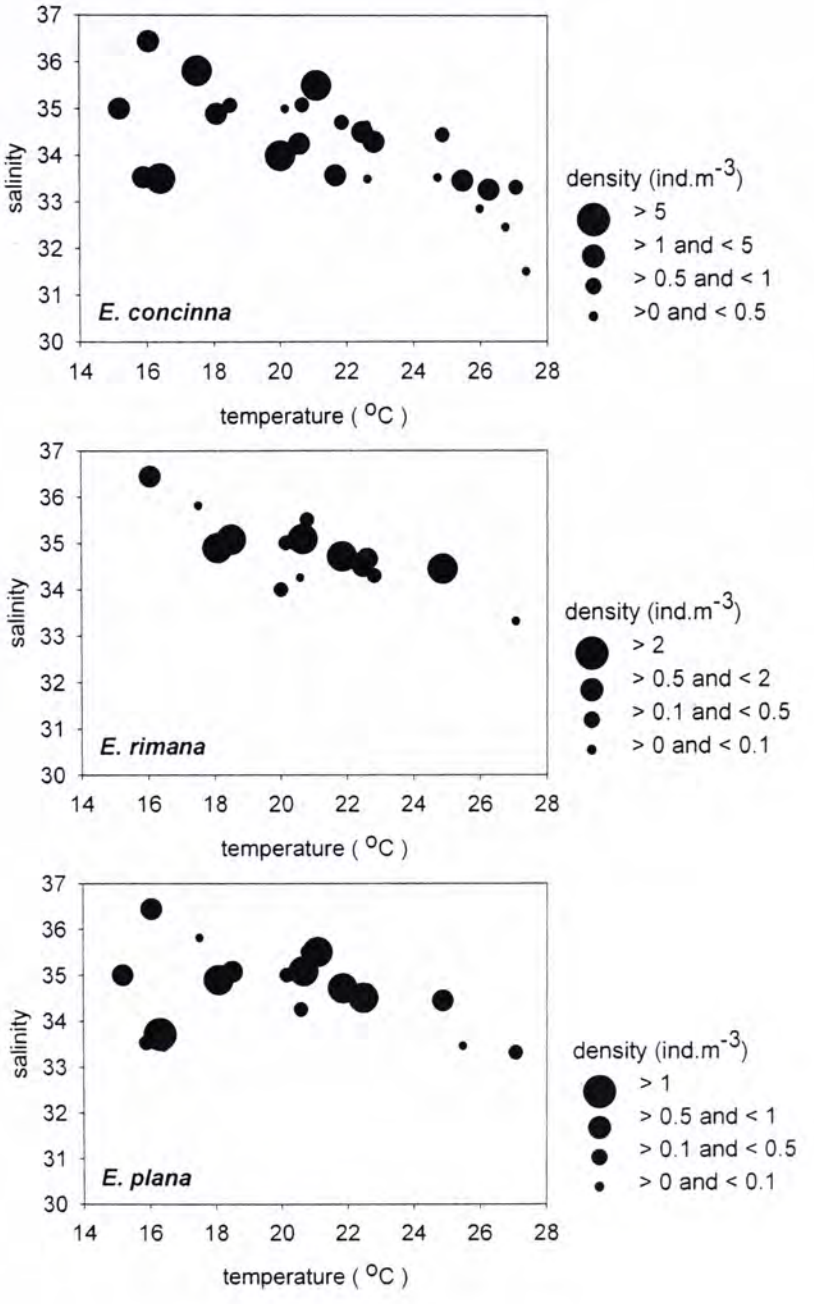

Figure 2.10 Occurrence of adult *Euchaeta (E. concinna*, *E. rimana* and *E. plana*) in waters of different surface temperature and salinity.

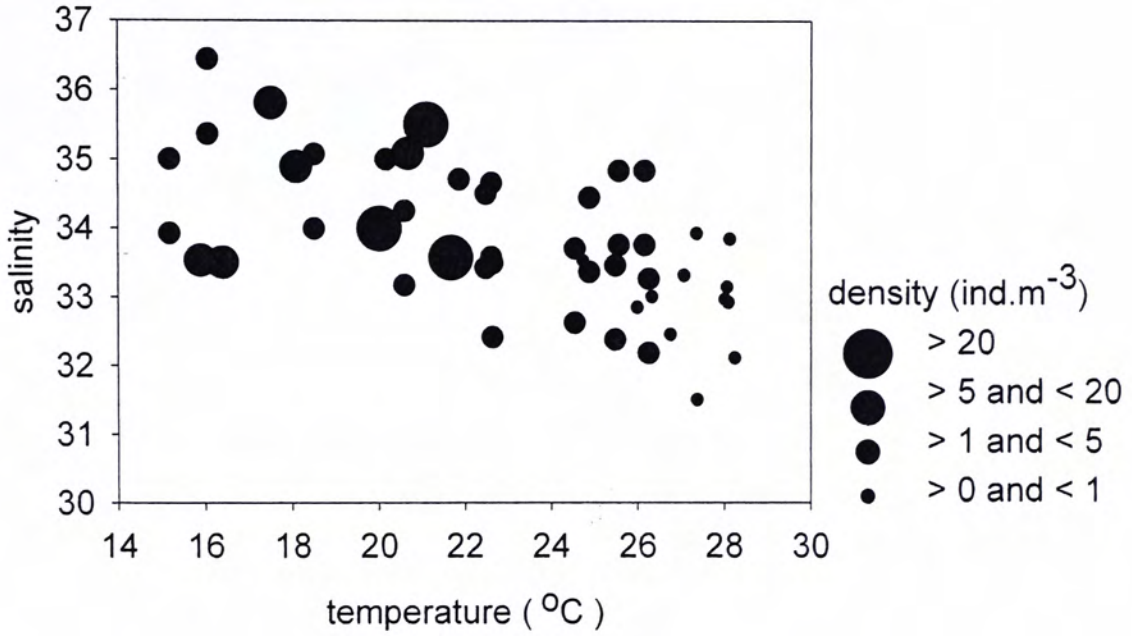

Figure 2.11 Occurrence of copepodids of *Euchaeta* spp. in waters of different surface temperature and salinity.

Table 2.5. Spearman Rank Order Correlation (r_s) between mean density of *Euchaeta* (adults of *E. concinna*, *E. rimana*, *E. plana* and copepodids of all species) and surface water temperature and salinity at six sampling stations. Sample size (n = 45) is the number of sampling conducted over the entire study period from July 2003 to June 2005.

Physical parameters	*Euchaeta*	r_s	*P*
Surface water temperature	*E. concinna*	-0.648	< 0.001
	E. rimana	-0.498	0.001
	E. plana	-0.713	< 0.001
	Copepodids	-0.761	<0.001
Surface water salinity	*E. concinna*	0.377	0.017
	E. rimana	0.625	< 0.001
	E. plana	0.615	< 0.001
	Copepodids	0.533	<0.001

2.4 Discussion

2.4.1 Diversity of *Euchaeta*

Three species of *Euchaeta* (*E. concinna*, *E. rimana* and *E. plana*) occur in the coastal waters of eastern Hong Kong. *E. concinna*, the most common species, comprises more than 70% of the total *Euchaeta* population. *E. rimana* and *E. plana*, the two less abundant species, constitute, respectively, only about 16% and 10% of the total *Euchaeta* population. Along the Chinese coast, these species have been described from the South China Sea, the Taiwan Strait, the East China Sea and the Yellow Sea (Chen and Zhang 1965; Chen and Shen 1974; Zheng *et al.* 1985). Park (1995) considered these species to be Indo-Pacific in distribution.

A total of four species of *Euchaeta* (*E. concinna*, *E. rimana*, *E. plana* and *E. indica*) have been recorded in Hong Kong's coastal waters in previous studies (Chen 1982; Chen *et al.* 2003; Chan 1995; Lee 2003). *E. concinna* and *E. plana* have been found in the western and southern parts of Hong Kong, while *E. rimana* was previously recorded in the southern part of Hong Kong (Chen 1982; Chan 1995; Chen *et al.* 2003; Lee 2003). *E. indica* is not found in this study, but it has been reported in

the western part of Hong Kong by Chen *et al.* (2003) and in the southern part of Hong Kong by Chan (1995). Chan (1995) conducted zooplankton sampling in Hong Kong's southern waters at biweekly intervals over a two-year period from January 1992 to January 1994, *E. indica* was only found in samples collected in February. Although *E. indica* is also known to be present in the Pearl River Estuary throughout the year, its density never exceeded 10 ind.m^{-3} (Chen *et al.* 2003). *E. indica* has never been found in zooplankton samples taken from the eastern part of Hong Kong.

Chen (1982) provided the only study on copepod assemblages in the coastal waters of eastern Hong Kong. Samples collected in April and May contained *Euchaeta concinna* and *E. rimana*. In this study, samples collected from same area, but in slightly deeper waters (S4, S5 and S6 in Mirs Bay), in the same months contains the two species reported by Chen (1982) as well as *E. plana* which has been found previously in other coastal areas of Hong Kong. Chen (1982) did not provide data on density, but his qualitative findings are consistent with results presented in this study in demonstrating that the abundance of *Euchaeta* is higher in deeper offshore waters than in shallow near-shore waters.

2.4.2 Seasonality in occurrence of *Euchaeta*

All three species of *Euchaeta* show strong seasonal pattern of occurrence. All three species are scarce in summer (June, July, August and September) and autumn (October and November) and become more abundant in winter (December, January, February and March) and spring (April and May). The seasonal pattern of copepodids is similar to that of adults. Occurrence of both adults and copepodids is influenced by water temperature and salinity. Dense populations are found only in winter and spring when temperature is low (16–24°C) and salinity is high (33–36). These findings are in agreement with those recorded previously in the western and southern parts of Hong Kong (Chen 1982; Chen *et al.* 2003; Lee and Chen 2003) and the southwestern part of Taiwan (Hwang *et al.* 2003).

Seasonality exhibited by *Euchaeta* in the temperate oceans of the East China Sea and the Yellow Sea differs dramatically from that recorded in subtropical seas around Hong Kong and Taiwan. *E. concinna*, the dominant *Euchaeta* species in the East China Sea and the southern part of the Yellow Sea, commonly reaches peak densities in summer and autumn (Chen and Zhang 1965). The less common species, *E. rimana* and *E. plana*, also peak in the same seasons (Chen and Zhang 1965). Cheng (1965)

pointed out that the numbers of *E. concinna* and *E. plana* in the Yellow Sea and the western part of the East China Sea increase substantially in summer and autumn when the Kuroshio Current moves warm and high salinity waters from offshore regions into the coastal areas of the East China Sea. Coastal seas off the northern tip of Taiwan are influenced by the Kuroshio Current year-round and by the China Coastal Current in winter. Not surprisingly, *Euchaeta* species including *E. concinna*, *E. rimana* and *E. plana* can be found in the area throughout the year and become particularly abundant in autumn and winter (Yang *et al.* 1999a) when water masses from the East China Sea flow towards Taiwan. *E. rimana* becomes the dominant species in winter, comprising 67% of the total copepod assemblages and reaching densities up to 40 ind.m^{-3} (Yang *et al.* 1999b).

2.4.3 Water movement and *Euchaeta* populations

Copepodids of all stages (C1, C2, C3, C4 and C5) are most abundant in December and January, although no clear pattern in cohort development is detected during the two-year sampling period. Although copepodids were not identified to species, this finding suggests that various species of *Euchaeta* are not indigenous to the coastal waters of Hong Kong, but are transported into the study area by water

currents. *Euchaeta concinna* is the dominant *Euchaeta* species in the East China Sea (Chen and Zhang, 1965). It can be speculated that *E. concinna* is transported with *E. rimana* and *E. plana*, the two less common species, from the East China Sea into the South China Sea via the Taiwan Strait by the China Coastal Current during winter when the northeast monsoon is in full strength.

Abundance and distribution of copepods are known to be influenced by hydrographic conditions (Boucher *et al.* 1987; Shih and Chiu 1998). Several previous studies have shown that copepod assemblages from the East China Sea and the Yellow Sea are transported into the southern coast of China during the northeast monsoon period between December and March (Chen 1982; Lee and Chen 2003; Yang *et al.* 2004; Hwang and Wong 2005). Lee and Chen (2003) have proposed that *Euchaeta plana* found in the coastal waters of Hong Kong in winter is carried into the area by the China Coastal Current. Cluster analysis of copepods samples collected in the Taiwan Strait revealed that *Euchaeta* belongs to communities associated with both the China Coastal Current and the Kuroshio Current (Yang *et al.* 2004). Species of *Euchaeta* comprise 16% of the copepod assemblage associated with the China Coastal Current and about 4% in the copepod assemblages associated with the Kuroshio Current. This result suggests that the distribution of *Euchaeta* in the Taiwan Strait is affected by

water circulation in the region. Hwang and Wong (2005) have also found that the peak occurrence of *Calanus sinicus* in northern Taiwan in December and in Hong Kong in February and March coincides with the intrusion of cold water masses into the southern part of China. These investigators further concluded that *C. sinicus* is carried into the coastal waters of Taiwan and Hong Kong from its population centers in the Yellow Sea and the East China Sea by the China Costal Current during the northeast monsoon period in winter.

2.4.4 *Euchaeta* populations in Tolo Habour and Mirs Bay

Adults and copepodids of *Euchaeta concinna*, *E. rimana* and *E. plana* are found in both Tolo Harbour and Mirs Bay. No adults of *E. rimana* are found at S1 in the inner part of Tolo Harbour. These observations suggest that *Euchaeta* is more common in the offshore waters of Mirs Bay than in the shallow and semi-enclosed waters of Tolo Harbour.

Tolo Harbour opens into the Mirs Bay through a narrow channel. Mirs Bay, on the other hand, is continuously influenced by water currents from the South China Sea. If *Euchaeta* is transported into Mirs Bay and then Tolo Harbour by water currents,

then the scarcity of *Euchaeta* in Tolo Harbour can be explained by loss during physical transport.

In addition to physical factors, trophic interactions may influence the abundance of *Euchaeta* in Tolo Harbour. Food web interactions have been shown to influence the population structure and behaviour of marine cladocerans in Tolo Harbour (Wong *et al.* 2004). The copepod communities in the eutrophic environments of Tolo Harbour are dominated by small copepods such as *Parvocalanus crassirostris* and *Paracalanus parvus* (Wong *et al.* 1993). Abundance of small calanoid copepods indicates that carnivorous copepods of the family *Euchaetidae* are not limited by food (Øresland 1991; Øresland and Ward 1993; Yen 1982, 1991). Chang *et al.* (2004) proposed that the density of large copepods is controlled directly by fish, while the density of the small copepods is controlled by invertebrate predators. Fish predation may be the reason for the disappearance or scarcity of *Euchaeta* in Tolo Harbour and other inshore areas of Mirs Bay. Dense populations of larval and juvenile black seabream (*Acanthopagrus schlegeli*) and Japanese seaperch (*Lateolabrax japonicus*) appear in Tolo Harbour during late winter and spring (Nip *et al.* 2003) when large copepods such as *Euchaeta* and *Calanus sinicus* also appear in Hong Kong's coastal waters. The impact of these fish on *Euchaeta* is unknown, but results of gut content analysis

showed that copepods and cladocerans are their most important food (Nip *et al.* 2003). *Pareuchaeta antarctica* has been reported as the major food for midwater fish in the Antarctic Peninsula (Hopkins 1985). *E. rimana* is bigger that *E. concinna* and *E. plana.* Susceptibility of copepods to visual predators increases with size. This may explain the absence of *E. rimana* at S1 in inner Tolo Harbour.

The low abundance of *Euchaeta* populations in Tolo Harbour and inshore areas of Mirs Bay could be because of (1) lack of refuge for this large copepod to avoid the visual predators and/or (2) high density of planktivorous fishes.

Light is crucial to the detection and capture of prey by visual predators such as planktivorous fish (Sørnes and Aksnes 2004). Water depth increases from Tolo Harbour (14 – 20 m) to Mirs Bay (21 – 30 m). *Euchaeta* may not be able to avoid fish in daytime by diel vertical migration in the shallow waters of Tolo Harbour. Our results, however, show that light intensity along water column decreases more rapidly in Tolo Harbour than in Mirs Bay, probably because of the high turbidity caused by the higher algal biomass. In Tolo Harbour, light intensity is reduced by > 90% (light refractive index < 0.1) at 10 m. In Mirs Bay, the same reduction in light intensity occurs at 15 m.

Threshold of light intensity for planktivorous fish to feed varies among different fish species and with prey size. Literature values include those of 0.925 $\mu mols^{-1} m^{-2}$ for the freshwater fish *Menidia beryllina* feeding on *Daphnia* (Wurtsbaugh and Li 1993), 1.9×10^{-5} $\mu mols^{-1} m^{-2}$ for herring (*Clupa harengus*) feeding on mixture of *Calanus finmarchicus*, *Pareuchaeta norvegica*, *Oithona similes*, *Balanus* sp. nauplii and crustacean nauplii (Batty *et al.* 1990), 5×10^{-5} $\mu mols^{-1} m^{-2}$ for walleye pollock (*Theragra chalcogramma*) and 5×10^{-7} $\mu mols^{-1} m^{-2}$ for sablefish (*Anaplopoma fimbria*) feeding on *Artemia* (Clifford and Bori 1999), and 8.2×10^{-8} $\mu mols^{-1} m^{-2}$ for Atlantic mackerel (*Scomber scombrus*) feeding on mixture of copepods (*Calanus finmarchicus* C1-C6, *Centropages typicus* C4-C6 and C4-C6 *Paracalanus* sp. and *Clausocalanus*) (Macy *et al.* 1998). In this study, light intensity in the bottom layers of Tolo Harbour and Mirs Bay is recorded to be around 1×10 $\mu mols^{-1} m^{-2}$. This implies that the shallow waters of Tolo Harbour and Mirs Bay do not provide sufficiently dark environment for large copepods to avoid fish during the day. Indeed, advantage gain from staying in the bottom layer in Tolo Harbour is the same as in Mirs Bay. Compared to Mirs Bay, the absence or scarcity of *Euchaeta* in Tolo Harbour is apparently not because of the lack of refuge to avoid visual predation.

Many investigators (Romen *et al.* 1993; Breitbery *et al.* 1997; Decker *et al.* 2003; Marcus 2004) have proposed that the development of hypoxia or anoxia in the bottom layers of eutrophic waters forces copepods to stay in the oxygenated waters in the upperparts of the water column. Large species which cannot tolerate low oxygen conditions is restricted to the oxygenated surface layers and becomes more exposed to visual predators. During this study, stratification of water column was recorded only in Tolo Harbour. In addition, hypoxia (< 2 mg L^{-1}) and anoxia (< 1 mg L^{-1}) in bottom waters were recorded only in the summer when *Euchaeta* was extremely rare (Figure 2.3). Copepods can tolerate oxygen concentrations as low as 1–2 mg L^{-1} (Roman *et al.* 1993; Stalder and Marcus, 1997). Indeed, copepods such as diapausing *Calanus pacificus* (Alldredge *et al.* 1984, 0.2 mg DO L^{-1}) and *Lucicutia grandis* (Wishner *et al.* 2000, < 0.15 mg DO L^{-1}) live in water of extremely low oxygen levels. Evidently, the scarcity of *Euchaeta* in Tolo Harbour is not a consequence of anoxia / hypoxia.

No data are available on the density of planktivorous fish in Tolo Harbour and Mirs Bay. For many years, however, Tolo Harbour has been an important site for the collection of juvenile fish for grow-out in local fish culture farms in Hong Kong (Wilson 1997). The density of copepods is higher in the nutrient-rich inshore areas with limited water circulation than in the offshore open waters (Chen 1982). As food

availability is extremely important to the recruitment success of fish, it can be argued that the shallow waters of Tolo Harbour may be a more useful nursery ground for fish than the offshore waters in Mirs Bay. Intensive activities of fish farmers in Tolo Harbour suggest that the area supports bigger populations of larval and juvenile fish than Mirs Bay. Planktivorous fish may exert stronger influence on the composition and abundance of *Euchaeta* populations in Tolo Harbour than in Mirs Bay.

2.5 Conclusions

Three species of *Euchaeta* (*E. concinna*, *E. rimana* and *E. plana*) occur in the eastern waters of Hong Kong. *Euchaeta concinna* is the most abundant species and comprises > 70% of all copepods of the genus *Euchaeta*.

All three species show strong seasonality in occurrence. *Euchaeta concinna* reaches peak density in winter, while *E. rimana* is abundant in spring. *E. plana* is common in both winter and spring. Low densities and lack of distinctive seasonal patterns in the occurrence of copepodids suggest that copepods of the genus *Euchaeta* are not indigenous to the local waters, but instead are carried into local area by ocean currents.

Densities of all *Euchaeta* species and its copepodids are highest in the offshore waters of Mirs Bay and decrease towards Tolo Harbour. The absence and scarcity of *Euchaeta* in Tolo Harbour and in inshore areas of Mirs Bay can be explained by: (1) loss during the physical transport from the open ocean to the semi-enclosed and poorly flushed inner part of Tolo Harbour, and (2) high fish predation pressure in Tolo Harbour. Large copepods depend on diel vertical migration to avoid visual predators.

Availability of refuge for *Euchaeta* in Tolo Harbour to avoid visual predator in daytime is discussed. *Euchaeta* is not excluded from Tolo Harbour by the lack of refuge, rather its scarcity or absence is because of the high density of planktivorous fish.

CHAPTER 3 DIEL VERTICAL DISTRIBTUION AND FEEDING ACTIVITIES OF *EUCHAETA CONCINNA* IN MIRS BAY

3.1 Introduction

3.1.1 Diel vertical migration (DVM)

Diel vertical migration (DVM) is a widespread phenomenon which is known to exist in many taxa of planktonic animals (Enright 1977; Pearre 1979). The typical pattern of DVM is that the migrating animals spend the day in deep waters and ascend to the surface layer at night (Lampert 1989). DVM in zooplankton is a flexible behaviour which is influenced by environmental factors such as light condition (Forward *et al.* 1984), presence of predators (Neill 1990; Bollens and Frost 1991b; Dini & Carpenter 1991), types of predators (Ohman 1990) as well as susceptibility of body condition of zooplankton towards visual predators including ovigerity (female with or without large and non-transparent egg sac) (Bollens and Frost 1991a) and energy reserve (body with or without coloured lipid droplets) (Hays *et al.* 2001; Vestheim *et al.* 2005). Of the several hypotheses proposed to explain the adaptive

significance of DVM, data supporting the predator avoidance hypothesis, which implies that DVM is a behavioral response for avoiding predators and predicts that occurrence of DVM in planktonic animals in the field is positively related to the abundance of predators, has been accumulated from laboratories studies (Fancett and Kimmerer 1985), field observations (Zaret and Suffern 1976; Stich and Lampert 1981; Gliwicz 1986; Frost 1988; Bollens and Frost 1989; Bollens and Stearns 1992) and manipulated field experiments (Bollens and Frost 1991b; Dini and Carpenter 1991).

Diel vertical distributions of the bathypelagic genus *Pareuchaeta* have been extensively studied and various patterns of DVM have been reported (Bollens and Frost 1991a; Mauchline 1995; Fleddum *et al.* 2001; Kaartvedt *et al.* 2002; Skarra and Kaartvedt 2003; Vesthrim *et al.* 2005). Strong normal DVM has been reported in *P. elongate* (formerly *Euchaeta elongata*), in the Dabob Bay of Washington. Individuals reside at depths ranging from 75 to 175 m during the day, and migrate to the upper 50 m of water column at night (Bollens and Frost 1991a). *P. norvegica*, a species in the Oslo-fjord of Norway, stays in the lower part of water column at 200 m during the day and only ascends to slightly shallower waters at night (Skarra and Kaartvedt 2003). *P. norvegica* in other Norwegian fjords exhibits significant bimodal DVM pattern. Individuals in the upperparts of the water column migrate, while some non-migrating

individuals remain in the bottom layers (Kaartvedt *et al.* 2002). These studies show that DVM in the family *Euchaetidae*, at least in the genus *Pareuchaeta*, is a dynamic behavioral trait which may be influenced by various environmental factors and physiological conditions. Compared with the genus *Pareuchaeta*, knowledge on the diel vertical distribution of the genus *Euchaeta*, which distributes widely in tropical and subtropical regions, is very limited and consists mostly of qualitatively description. Chen *et al.* (1980) noted that *E. concinna*, *E. rimana* and *E. plana* in the offshore area of the southeastern part of the East China Sea remain mostly in the bottom layer. Yang *et al.* (1999b) reported that *E. concinna* and *E. rimana* in the north of Taiwan are most common in depths of 0–50 m and 0–25 m, respectively.

3.1.2 Diel feeding rhythm

Apparent diel feeding rhythm in zooplankton has been reported for over half a century (Fuller 1937; Gauld 1953; Mackas and Bohrer 1976; Ishii 1990; Atkinson *et al.* 1992a) and the existence of diel feeding rhythm seems to vary from species to species (Mackas and Bohrer 1976; Peterson *et al.* 1990; Atkinson *et al.* 1992a, 1992b). Mackas and Bohrer (1976) described two types of diel feeding rhythm including the unimodal type with a single peak of gut content at night and the bimodal type with

peaks around sunset and sunrise. Although unimodal feeding rhythm is most frequently found, observation of bimodal feeding rhythm was not uncommon (Simard *et al.* 1985; Ishii 1990).

Several hypotheses have been proposed to explain the cause and adaptive significance of diel feeding rhythm. Epipelagic environments are characterized by greater food availability but higher risks of predation. Both food supply and predation risk decrease with increasing water depth. As a consequence of DVM, migrating copepods move between the food-abundant surface layer and the food-scarce bottom layer and diel changes in feeding activities occur. On the other hand, findings of diel variation in gut contents in non-migratory copepods show that diel feeding rhythm can be independent of DVM (Dagg *et al.* 1989; Peterson *et al.* 1990). Diel feeding rhythm is believed to be a mechanism to avoid accumulation of body pigments in daytime (Kleppel *et al.* 1985; Dagg *et al.* 1989). As copepods are the major prey of the planktivorous fishes, actively feeding copepods are more susceptible to the visual predators as a result of their movements and pigmented gut. Bollens and Stearns (1992) demonstrated the adaptive significance of diel feeding rhythm as a predator avoidance strategy. Copepods exposed to fish have significantly lower level of daytime gut fullness than copepods not exposed to fish.

Active feeding activity at night has been frequently observed in *Pareuchaeta* in previous laboratory and field studies. Yen (1982) investigated the feeding periodicity of *P. elongata* in laboratory experiment under dark condition and showed that feeding rates were significantly higher during the night than the day. Skarra and Kaartvedt (2003) also reported that the most active feeding activity of *P. norvegica* in the field was found in individuals captured from between 50 and 100 m at night. Kaartvedt *et al.* (2002) further related the feeding activity to the diel vertical distribution of *P. norvegica*. Higher feeding activity was found in individuals collected from the upper 100 m of the water column at night, during nocturnal ascend.

3.1.3 Dietary composition and prey selectivity

Copepods of the family *Euchaetidae* are strictly carnivorous, feeding predominantly on other small copepods (Øresland 1991; Yen 1991; Fleddum *et al.* 2001). Natural diets of four species of *Pareuchaeta* (*P. antarctica*, *P. farrani*, *P. rasa* and *P. biloba*) in South Georgia Island near the Antarctic have been studied (Øresland 1991; Øresland and Ward 1993). Copepods of various sizes made up 46–99% of all food items in the gut content. Other food items included polychaetes, chaetognaths,

krills and other crustaceans. Øresland (1995) examined the indigestible copepod mandibles left in the gut content and reported that the small copepods including *Oncaea* spp. and *Microcalanus pygmaeus* formed the main food of *P. antarctica*. Prey size has been shown to strongly influence dietary selectivity of *P. elongata* in both laboratory experiments and field studies (Yen 1982, 1983, 1985a). Yen (1985a) reported that *P. elongata* showed the highest predation rates on copepods ranging from 0.65–1.0 mm in prosome length and the prosome length of the copepod prey was usually 70% the length of the second basipodal segment of the maxilliped for adult *P. elongata* and its late copepodid stages (C4 and C5). Similarly, *P. antarctica* exhibited the highest feeding rates on prey copepods having prosome length of 1.2 mm and the size of preferred prey was about 65% the length of the second basipodal segment of the maxilliped for adult *P. antarctica* (Yen 1991). Although size is a major determining factor in the dietary selectivity of *P. elongata*, species-specific behavioral differences are also important. In general, *Pseudocalanus* spp. are preferred over small cyclopoid copepods (Greene and Landry 1985; Yen 1985a).

3.1.4 Predation impact

In the zooplankton, predation by invertebrate carnivores is recognized to have a significant impact on the distribution and population dynamics of prey communities in both freshwater (Dodson, 1974; Kerfoot, 1975, 1978; Neill 1981; Vega 1998) and marine ecosystems (Fulton 1982, 1983; Ohman *et al.* 1983). Although knowledge has been accumulated on feeding behaviour, size-selective feeding and functional response for many marine carnivorous copepods (Landry 1978; Landry and Fagerness 1988; Yen 1983, 1985a; Greene and Landry 1985), few studies have assessed the mortality of natural prey population due to predation by the predatory copepods such as the strictly carnivorous family *Euchaetidae*. To our understanding, only one recent study in feeding of *Pareuchaeta norvegica* in the Skagerrak has investigated the regulatory role of this carnivorous copepod on the populations of small copepods (Tönnesson *et al.* 2006). It was showed that *P. norvegica* removed 2.0–6.5% of prey copepod population daily and the predation impact was 10- to 100-fold greater than those imposed by chaetognaths in the same study site. Uye and Kayano (1994) estimated the predation impact of the carnivorous copepod *Tortanus* spp. on copepod assemblages in Fukuyama Harbour, Japan using laboratory-determined functional response. The estimated predation impact was small with only < 2.7% of the prey

population consumed daily by the predator. Hooff and Bollens (2004) investigated the predation impact of *Tortanus dextrilobatus* in the San Francisco Estuary and concluded that this invertebrate predator can play a significant role, at least seasonally, on the population dynamics of small copepods by imposing maximum predation impacts exceeding 20, 65 and 25% for *Oithona davisae*, *Acartia* sp. and all copepods, respectively.

3.1.5 Study area

Euchaeta concinna is the most common and widespread species of the family Euchaetidae in the coastal waters of Hong Kong and southern China (Chen 1982; Chan 1995; Chen *et al.* 2003; Hwang *et al.* 2003; Lee 2003; Lo *et al.* 2004; Yang *et al.* 2004). In the coastal waters of eastern Hong Kong, *E. concinna* is the most abundant species of Euchaetidae. *E. concinna* reaches peak abundances of >10 ind. m^{-3} during the winter in Mirs Bay.

3.1.6 Objectives of study

The objectives of this study are: (1) to describe the diel vertical distribution and feeding rhythm of adult *Euchaeta concinna* in Mirs Bay, (2) to determine the dietary composition and prey selectivity of adult female *E. concinna*, and (3) to estimate the predation impact of female *E. concinna* on copepod assemblages.

3.2 Materials and Methods

3.2.1 Field sampling

DVM of *Euchaeta concinna* was studied at S5 in Mirs Bay (Figure 2.1) on 6–7 January 2005 when preliminary survey on the morning of 6 January 2005 revealed that the density of *E. concinna* was > 10 ind.m^{-3}. Water depth at S5 was about 28 m. Duplicate zooplankton samples (from separate vertical hauls) were taken from 0–5 m, 5–10 m, 10–15 m, 15–20 m and 20–25 m with a plankton net (50 cm mouth diameter, 125 μm mesh size) at 1200, 1600, 2000, 2400, 0400 and 0800 h. All samples were immediately preserved in 4% buffered formaldehyde-seawater solution. Vertical profiles of temperature, salinity and DO were measured at noon and midnight with Hydrolab H20 water analysis system. Light intensity was measured at noon only with light meter and was expressed as light refractive index which represents the ratio of light intensity in the water to light intensity in the air.

3.2.2 Laboratory analysis

In the laboratory, *Euchaeta concinna* was identified according to Park (1995) and densities of adults were estimated by counting entire samples. Male and female *E. concinna* were identified according to the morphological characteristic of their reproductive structures. Females with (ovigerous) and without egg sac (non-ovigerous) were counted separately. Copepod densities were estimated by counting at least 5% of each sample. At least 100 copepods from each sample were identified to genus level according to descriptions of Zheng *et al.* (1985) to provide information on species compositions.

Yen (1991) reported that adult males of congener species *Pareuchaeta antarctica* showed no feeding activities in laboratory feeding experiments. As the oral appendages of adult male *Euchaeta concinna* are highly reduced as compared to the female, which is sign of non-feeding life style of copepod, only feeding activities of the females was investigated in this study. Ten female *E. concinna* from each sample were sorted out and the entire digestive tract was dissected under a stereomicroscope according to the method of Øresland (1991). The diameter (d) and length (L) of the dissected stomach and stomach content were measured under the stereomicroscope.

The volumes of the stomach and the stomach content were estimated using formula $\pi(d/2)^2L$. The stomach content in the anterior part of the digestive tract was examined under a light microscope and the dietary remains were identified as far as possible to the lowest taxon, using identifiable parts such as the mandibles. Gut fullness index was estimated from the ratio of the volume of stomach content to the total volume of the stomach.

3.2.3 Laboratory feeding experiment

Feeding of female *Euchaeta concinna* was studied in laboratory. Live copepods were collected by vertical hauls at S5 and immediately returned to the laboratory in 10-L plastic bottles. Adult females of *E. concinna* were sorted and starved for at least 24 h in 125-μm filtered seawater at 20°C in large aquaria. Females in good conditions and active swimming were then transferred to 1-L fleakers in water baths with temperature adjusted to 18°C (similar as water temperature in the field). Five common small copepods, *Paracalanus/Parvocalanus* (*Paracalanus parvus, Paracalanus aculeatus* and *Parvocalanus crassirostris*), *Oithona* spp. (*O. rigida, O. simplex, O. brevicornis, O. attenuate*) and *Acrocalanus* (*A. gibber, A. gracilis*), Corycaeus spp. (*C. affinis, C. concinnus, C. dahlia, C. gibbulus, C. subtilis*) and Oncaea spp. (*O. conifera,*

O. media, O. mediterranea) were chosen as prey. As sorting small copepods alive under stereomicroscope was time-consuming, prey were identified to genus level only. Based on their relative abundances in the field, *Paracalanus / Parvocalanus, Acrocalanus* and *Oithona* were tested at prey concentrations of 10, 20 and 30 prey L^{-1} while *Corycaeus* and *Oncaea* at 3, 5 and 10 prey L^{-1}. Single predator provided with tested concentration of prey copepod was allowed to feed in darkness in 1-L fleakers. After 24 hours, the number of surviving prey was counted. Missing prey was assumed to be lost to predation. Daily feeding rate (DFR, prey.predator^{-1} day^{-1}) were calculated. At least five replicates and two controls (i.e. no predator) were conducted for each tested prey concentrations. Recovery in control bottle was higher than 99% in this study.

Another laboratory feeding test was conducted to find out the digestion time of female *Euchaeta concinna* on major prey copepods. Methods for live copepods collection, sorting and acclimation were same as above. Before start of experiments, single female *E. concinna* was put in a 1-L fleaker and was allowed to acclimatize for 1 h. Two groups of small copepods, *Paracalanus/Parvocalanus* and *Acrocalanus* were used as prey. Sorted prey copepods were stained by neutral red for about 30 min and washed with 125-μm filtered seawater. Thirty live, stained preys were added to

each fleaker containing a single predator. Female *E. concinna* was allowed to feed and was immediately transferred to a fleaker with no prey items after ingesting prey. Digestion time was defined as the duration between prey capture and egestion of a colored fecal pellet by the predator. The digestion time of *E. concinna* for each group of prey was obtained by observing 10 female individuals.

3.2.4 Data analysis

To compare the vertical distribution of the predator and prey, weighed mean depth (*WMD*, m) was calculated from (Worthington 1931):

$$WMD = (\Sigma D_i d_i) / \Sigma D_i$$

where d_i is the water depth of samples i collected from and D_i is the density of copepod in sample i.

Prey selectivity was calculated using the electivity measure (α) of Chesson (1978). Electivity for prey item i (α_i) was calculated with the equation:

$$\alpha_i = (r_i / p_i) / (\Sigma r_i / p_i)$$

where r_i and p_i were the proportion of prey item i in gut of predator and in the environment, respectively. The measure (α) was converted to an electivity index (ε) using the equation (Chesson 1983):

$$\varepsilon_i = (m\alpha_i - 1) / [(m\alpha_i - 2)\alpha_i + 1]$$

where m is the number of prey items and the value of ε ranges from −1 to +1. Positive value indicates selection for and negative value selection against the prey item.

Feeding rate (I_t, prey individual^{-1} time interval^{-1}) of female *Euchaeta concinna* at sampling time interval t with a duration of 4 h was estimated by the equation:

$$I_t = 4G_t / d$$

where G_t is the number of prey per female *E. concinna* collected at time interval t and d is digestion time in hours.

The daily predation impact (*DPI*, % of prey removed day^{-1}) of female *Euchaeta concinna* on a particular prey was then calculated by:

$$DPI = \Sigma [(I_t N_t / P_t) 100]$$

where I_t is the feeding rate of female *E. concinna* at time interval *t*; N_t and P_t are, respectively, the densities of female *E. concinna* and prey at time interval *t*.

Data collected from replicate samples was presented as mean value with standard deviation (SD). Differences between multiple samples ($n > 2$) were tested using ANOVA. To compared *WMD* or *PS* between day (1200, 1600 and 0800 h) and night (2000, 2400 and 0400 h) samples, pooled data collected from different times were tested by Student's *t*-test. In all cases, nonparametric tests were used if assumptions of normality (Normality Test) or homogeneity of variance (Equal Variance Test) were not met. The alpha level was 0.05. All statistical tests were conducted using software SigmaStat 3.1 and statistical results on ANOVA (or nonparametric ANOVA) are included in the Appendices.

3.3 Results

3.3.1 Hydrography

The vertical profiles of water temperature, salinity and dissolved oxygen (*DO*) are presented in Figure 3.1. Water was well mixed and no stratification of the water column was observed. Averaged over the entire water column, mean water temperatures, salinity and DO in daytime were 17.6°C, 33.7 and 7.46 mg L^{-1}, respectively. Conditions remained the same at night, with water temperature at 17.3°C, salinity at 33.9 and DO at 7.64 mg L^{-1}. Light intensity was measured at noon (Fig. 3.1). Light intensity was highest at the surface and decreased rapidly with increasing depth. Very little light was detected below 15 m.

3.3.2 Density of *Euchaeta concinna*

Diel vertical migration of *Euchaeta concinna* was studied at S5 on 6–7 January 2005. Over the entire water column, density of adult *E. concinna* at the sampling station was ~ 12 ind. m^{-3} (Table 3.1) and did not change significantly with time (One-way ANOVA, $P = 0.560$).

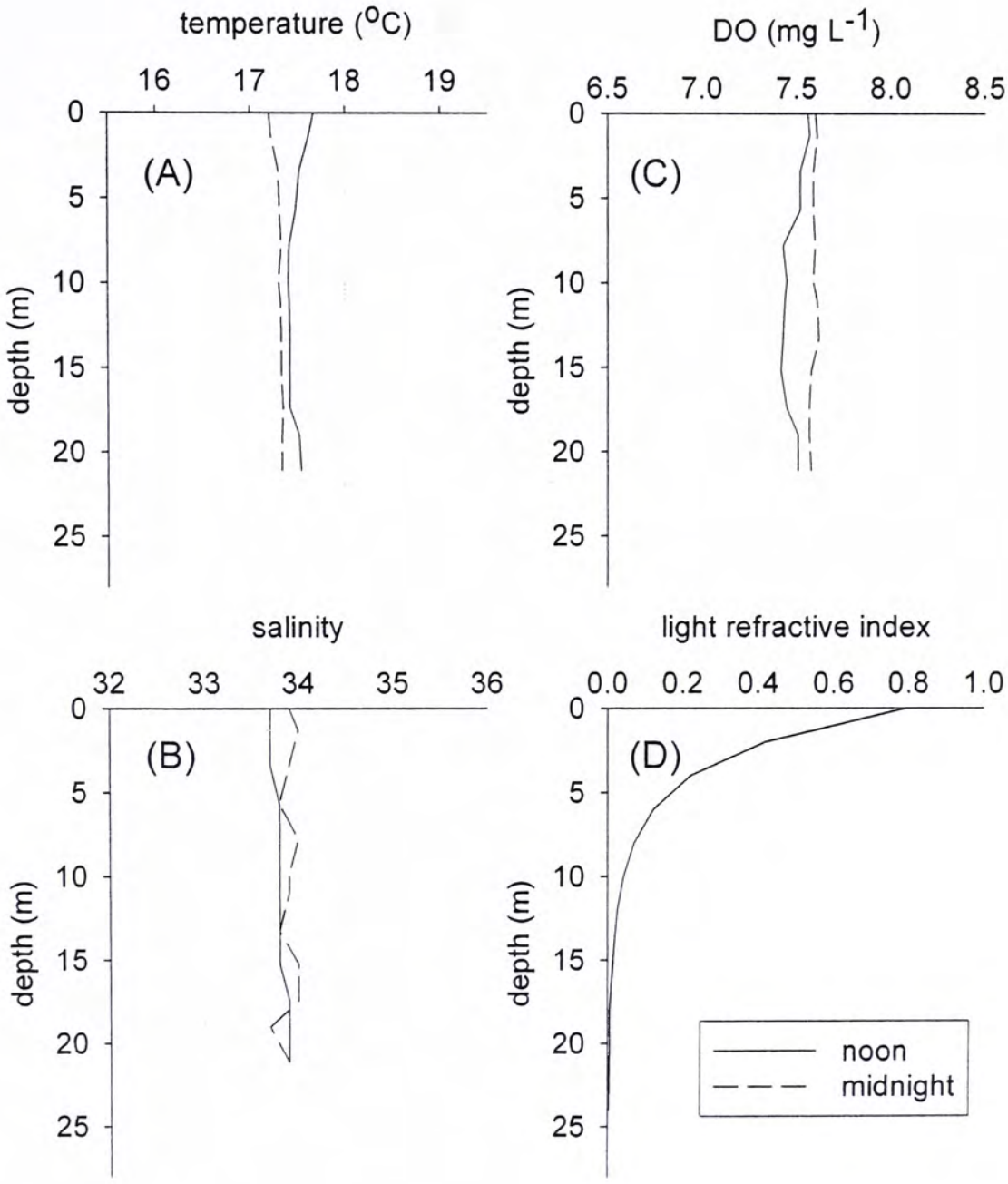

Figure 3.1 Vertical profiles of (A) temperature, (B) salinity, (C) DO and (D) light intensity (noon only) at noon and midnight on 6–7 January 2005.

Table 3.1 Density (mean ± SD) of adult *Euchaeta concinna* at S5 in Mirs Bay on 6–7 January 2005. Values were estimated from zooplankton samples taken by vertical hauls from bottom to surface.

Sampling interval	Density (ind.m^{-3})
1200 –1600 h	12.5 (± 3.6)
1600 – 2000 h	11.9 (± 2.5)
2000 – 2400 h	10.0 (± 2.9)
2400 – 0400 h	14.1 (± 0.7)
0400 – 0800 h	13.0 (± 0.8)
0800 – 1200 h	11.3 (± 0.7)
Overall mean	12.1 (± 1.4)

3.3.3 Diel vertical distribution

Diel patterns in the vertical distribution of *Euchaeta concinna* females and males are showed in Figure 3.2. During the afternoon from 1200 h to 1600 h, most of the females stayed below 10 m. The main part of the population was at 10–15 m at noon and 15–20 m at 1600 h. Few individuals were in the upperparts of the water column. An upward migration by adult females was detected after sunset. At 2000 h, the density of adult females increased to ~ 10 ind. m^{-3} at 0–5 m and 10–15 m. At the same time, < 5 ind. m^{-3} was recorded at 15–20 m and 20–25 m. A significant downward movement of the population occurred after midnight. From 2400 h to 0800, population tended to aggregate in the lower parts of the water column. Density at 20–25 m was ~20 ind. m^{-3} at 2400 h and > 15 ind. m^{-3} at 0400 h and 0800 h. Few *E. concinna* females were found in samples collected at 0–5 m and 5–10 m at 0800 h. Vertical migration pattern of males was similar to that of females. Ovigerous and non-ovigerous females also showed almost similar pattern of vertical migration (Fig. 3.3).

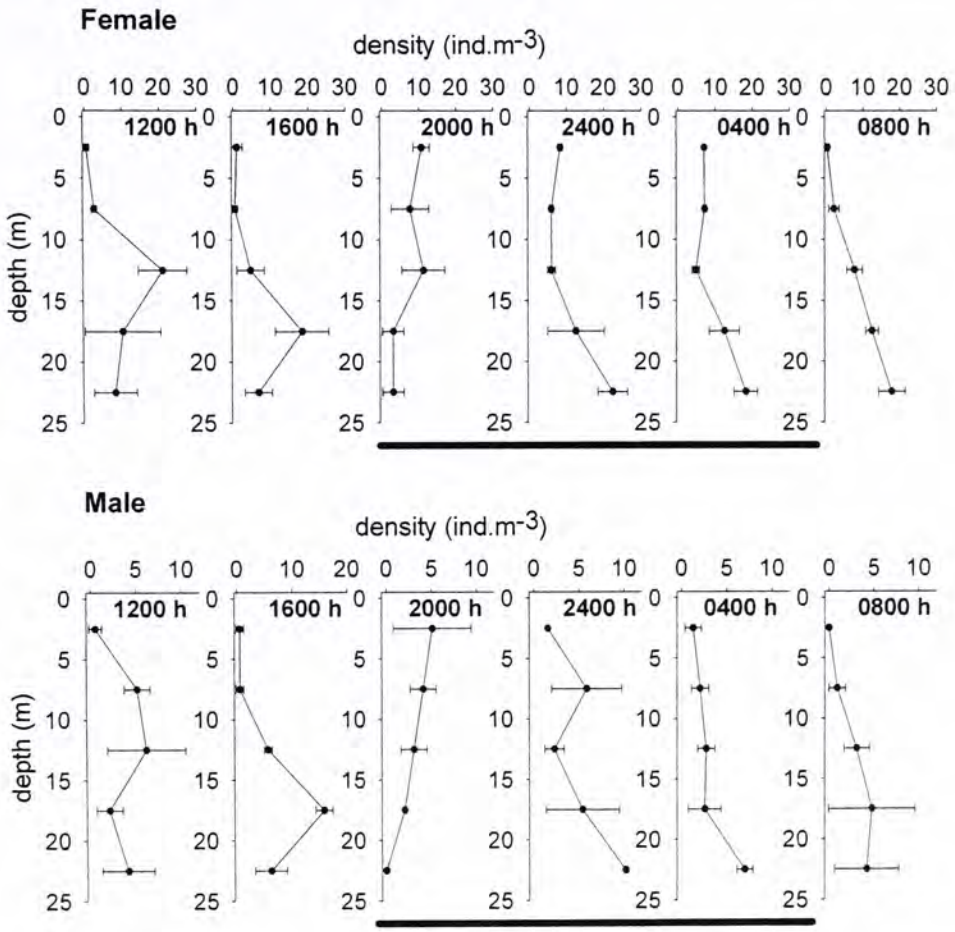

Figure 3.2 Diel variations in density (mean ± SD) of adult female and male *Euchaeta concinna* at different water depths. Dark horizontal bar represents nighttime.

Weighted mean depth (*WMD*) (Table 3.2) measures the water depth where the core of the population was located, while percentage at the surface (*PS*) (Table 3.3) measures the proportion of population that was located at the upperparts of the water column (0–5 m and 5–10 m). *Euchaeta concinna* was considered to have performed diel vertical migrations only if both *WMD* and *PS* were significantly different between day and night. *WMD* for both female and male *E. concinna* was significantly smaller at night than during daytime. Similarly, for both ovigerous and non-ovigerous females of *E. concinna*, *WMD* recorded at night was significantly smaller than that recorded during the day. *PS* for both female and male *E. concinna* were significantly higher at night than during the day. Similarly, *PS* for both ovigerous and non-ovigerous females of *E. concinna* were significantly higher at night than during the day. Therefore, it is concluded that adult *E. concinna* including males, ovigerous females and non-ovigerous females have performed diel vertical migration.

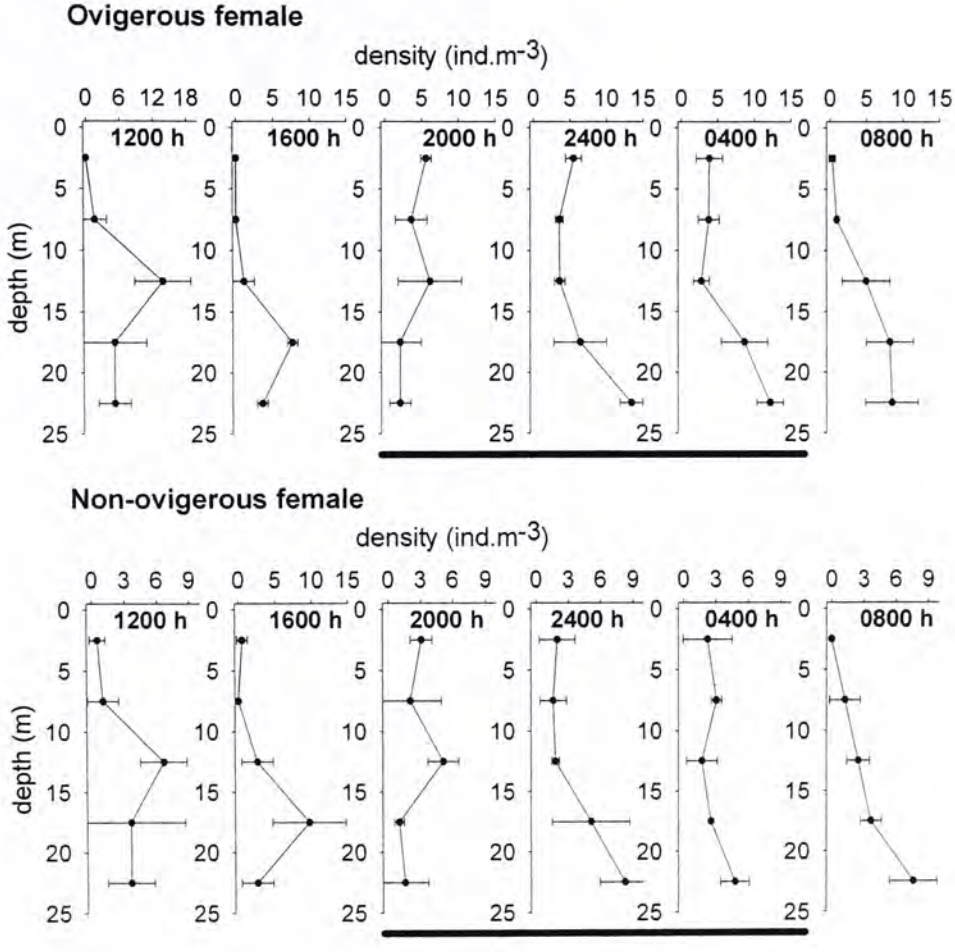

Figure 3.3 Diel variations in abundance (mean ± SD) of ovigerous and non-ovigerous female *Euchaeta concinna* at different water depth. Dark horizontal bar represents nighttime.

Table 3.2 Diel patterns in weighted mean depth (*WMD*) for adult *Euchaeta concinna* in Mirs Bay. *n* is the number of samples (day: 1200, 1600 and 0800 h; night: 2000, 2400 and 0400 h). * difference between day and night was tested by Student's *t*-test.

E. concinna	*WMD* (m)				
	Day		Night		
	n	mean (±SD)	*n*	mean (±SD)	*P* *
Female	6	16.8 (1.3)	6	12.8 (3.1)	0.014
Male	6	16.0 (1.4)	6	12.9 (3.1)	0.047
Ovigerous female	6	17.2 (1.9)	6	12.9 (3.2)	0.016
Non-ovigerous female	6	16.9 (1.4)	6	13.3 (3.1)	0.030

Table 3.3 Diel patterns in percent of population at surface (*PS*) for adult *Euchaeta concinna* in Mirs Bay. Surface refers to the upper 10 m of the water column. *n* is the number of samples (day: 1200, 1600 and 0800 h; night: 2000, 2400 and 0400 h). * difference between day and night was tested by Mann-Whitney Rank Sum Test.

	PS (%)				
E. concinna	Day		Night		
	n	mean (±SD)	*n*	mean (±SD)	*P* *
Female	6	6.1 (2.8)	6	38.3 (12.1)	0.002
Male	6	15.5 (16.4)	6	40.6 (20.7)	0.041
Ovigerous female	6	4.1 (5.6)	6	37.3 (14.5)	0.002
Non-ovigerous female	6	6.1 (7.4)	6	33.4 (9.6)	0.004

3.3.4 Diel feeding rhythm

The diel changes in the gut fullness of female *Euchaeta concinna* at different water depth are showed in Figure 3.4. Female tended to have empty guts during daytime (1200, 1600 and 0800 h). Feeding increased after sunset. An increase in gut fullness was observed in females collected from the upperparts of the water column (0–5 m, 5–10 m and 10–15 m) at 2000 h. The highest gut fullness index of 0.7 was recorded at 2400 h from females collected at 0–5 m. A definite decrease in gut fullness level was observed at 0400 h. Gut fullness of females at all depths returned to very low levels at 0800 h. Gut fullness of female *E. concinna* differed significantly between day and night but not among water depths (Two Way ANOVA, $P < 0.001$ and $P = 0.774$ respectively, no interaction). The highest gut fullness was recorded at 2400 h. These observations suggest that female *E. concinna* exhibited diel feeding rhythm and fed most actively at night.

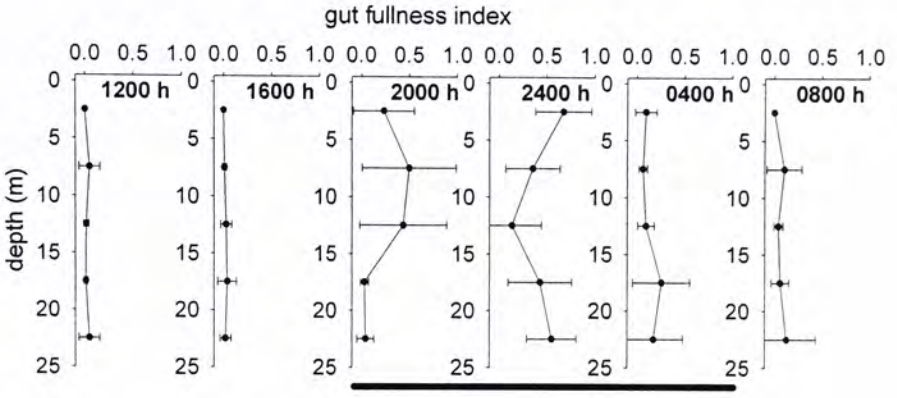

Fig 3.4 Diel changes in gut fullness index (mean ± SD) of adult female *Euchaeta concinna* collected at different depths. n = 10. Dark horizontal bar represents nighttime.

3.3.5 Dietary composition and prey selectivity

Copepods, which comprised about 40% of the gut contents, were the major prey of female *Euchaeta concinna.* Other common food items included unidentified eggs (~ 29%), unidentified items (~ 17%) and crustacean remains (~ 14%). All copepods found in the gut of female *E. concinna* were calanoid copepods. *Acrocalanus* (~ 50%) was the most common copepod prey, followed by *Paracalanus/Parvocalanus* (~ 30%), copepodids of *Canthocalanus* (~ 11%) and other calanoid copepods (mainly copepodids of *Centropages* and *Subeucalanus*) (~ 9%) (Fig. 3.5). Female *E. concinna* showed strong positive selection for *Acrocalanus*. *Paracalanus/Parvocalanus* was also positively selected. Copepodids of *Canthocalanus* and other calanoid copepods were negatively selected (Table 3.4).

3.3.6 Prey availability

Diel variations in the vertical distribution pattern of major prey (*Acrocalanus*, *Parvocalanus/Paracalanus* and copepodids of *Canthocalanus*) were compared with that of adult female *Euchaeta concinna* (Fig. 3.6). *Acrocalanus* and *Paracalanus /*

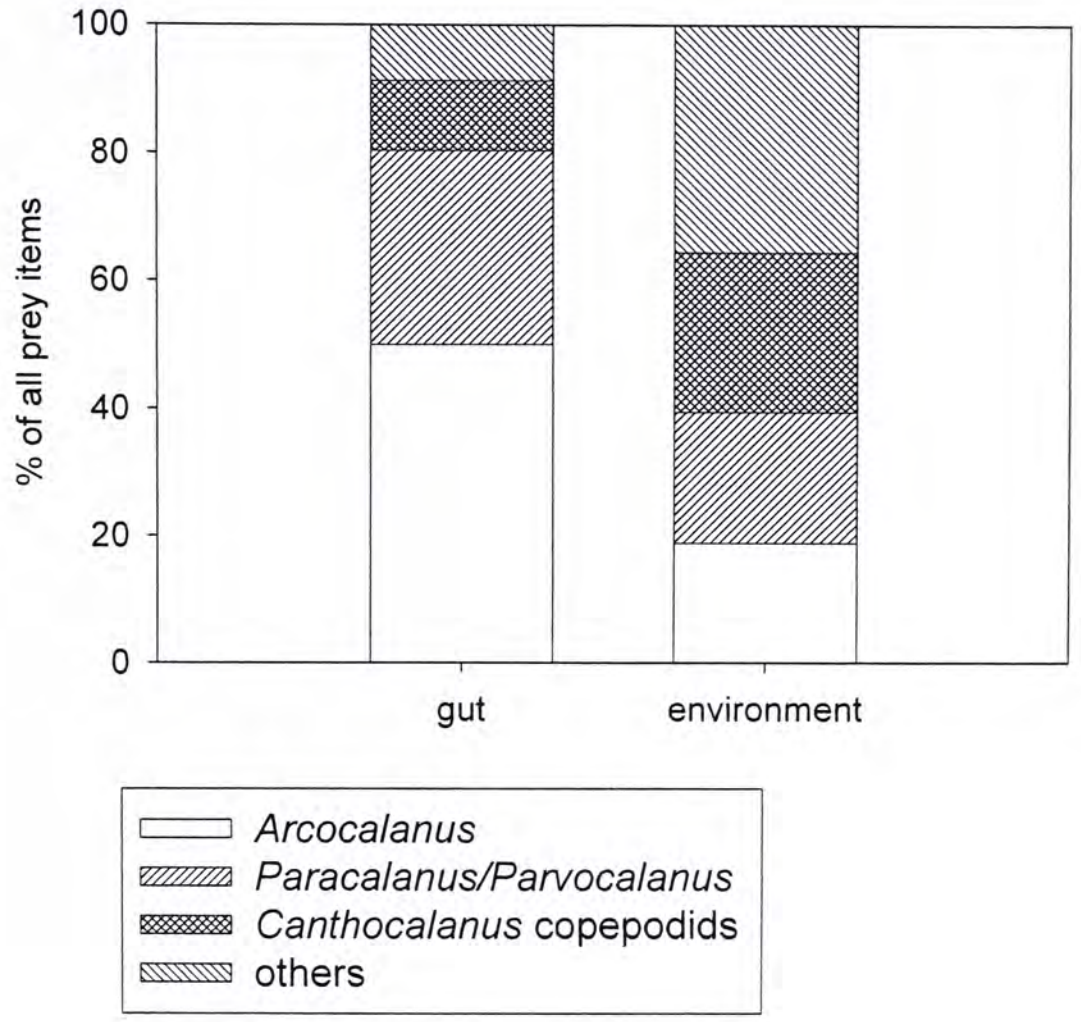

Figure 3.5 Composition of copepods in the environment and in the guts of adult female *Euchaeta concinna*.

Table 3.4 Selective feeding by adult female *Euchaeta concinna.* Copepods comprised about 40% of all prey items identified in guts of female *E. concinna.* Electivity index (ε) ranges from -1 to +1.

Prey	% of guts	% of all prey items in guts	% of all prey items in environment	ε
Acrocalanus	51.6	50.0	18.9	0.51
Paracalanus / Parvocalanus	32.3	30.4	20.5	0.21
Canthocalanus copepodids	12.9	10.9	25.0	-0.32
other calanoid copepods	9.66	8.7	35.7	-0.94

No. of gut dissected = 277
No. of gut containing copepod mandibles = 91
No. of mandible identified = 146

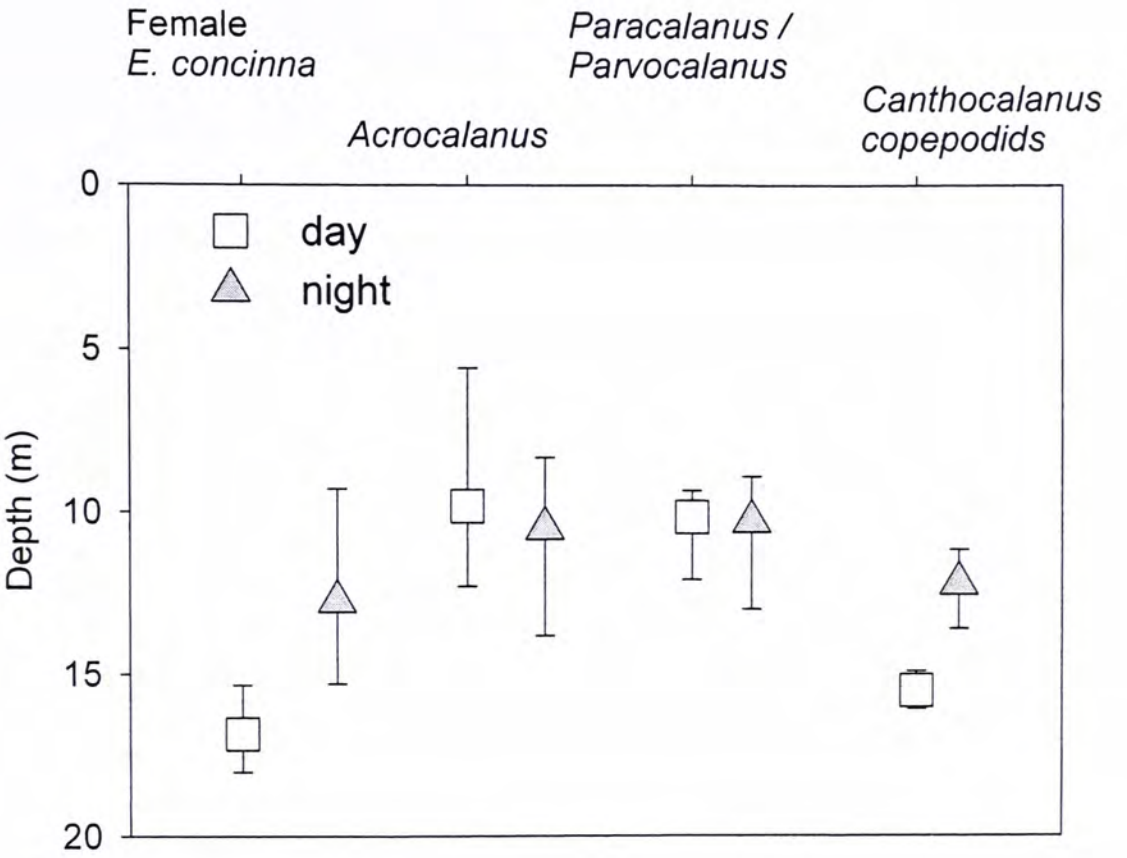

Figure 3.6 Weighed mean depth (*WMD*, mean ± range) of adult female *Euchaeta concinna* and other major copepods during day (1200 h, 1600 h and 0800 h) and night (2000 h, 2400 h and 0400 h).

Parvocalanus stayed at the upperparts of the water column during both day and night. In contrast, *Canthocalanus* copepodids seemed to reside in slightly shallower waters at night. The *WMD* for all three major groups of prey copepods did not differ significantly between day and night (Table 3.5). No significant differences between day and night were recorded in the *PS* for *Acrocalanus* and *Parvocalanus/ Paracalanus*, but the *PS* for *Canthocalanus* copepodids was significantly higher at night than during the day (Table 3.6). It can be concluded that *Canthocalanus* copepodids showed weak DVM, while *Acrocalanus* and *Parvocalanus/Paracalanus* did not. The vertical distribution of *Acrocalanus* and *Paracalanus/Parvocalanus* overlapped with that of female *E. concinna* at night (no significant difference between *WMD* of predator and preys, one-way ANOVA, $P = 0.933$), but not during the day (significant differences between *WMD* of predator and preys, one-way ANOVA $P < 0.001$ and Tukey test, both $P < 0.05$). In comparison, the vertical distribution of *Canthocalanus* copepodids appeared to overlap with that of female *E. concinna* during both day (no significant differences between *WMD* of predator and preys, one-way ANOVA, $P < 0.001$ but Tukey test, $P > 0.05$) and night (one-way ANOVA, $P = 0.933$). In conclusion, the vertical distribution of *E. concinna* females overlapped significant with those of their preferred prey (*Acrocalanus* and *Paracalanus/Parvocalanus*) only during the night.

Table 3.5 Diel patterns in weighted mean depth (*WMD*) of major prey copepods in Mirs Bay. *n* is the number of samples (day: 1200, 1600 and 0800 h; night: 2000, 2400 and 0400 h). * difference between day and night was tested by Student's *t*-test.

	WMD (m)				
	Day		Night		
Major prey copepods	*n*	Mean (±SD)	*n*	mean (±SD)	*P**
Acrocalanus	6	9.8 (3.4)	6	10.5 (2.9)	0.716
Paracalanus / *Parvocalanus*	6	9.9 (1.1)	6	10.3 (7.2)	0.893
Canthocalanus copepodids	6	15.5 (0.8)	6	12.2 (13.4)	0.562

Table 3.6 Diel patterns in percent at surface (*PS*) of major prey copepods in Mirs Bay. Surface refers to the upper 10 m of the water column. *n* is the number of samples (day: 1200, 1600 and 0800 h; night: 2000, 2400 and 0400 h). * difference between day and night was tested by Mann-Whitney Rank Sum Test.

	PS (%)				
	Day		Night		
Major prey copepods	*n*	mean (±SD)	*n*	Mean (±SD)	*P**
Acrocalanus	6	55.8 (23.6)	6	54.0 (16.7)	0.699
Paracalanus / *Parvocalanus*	6	56.6 (6.1)	6	54.2 (11.1)	0.818
Canthocalanus copepodids	6	21.8 (7.6)	6	41.2 (11.5)	0.026

3.3.7 Feeding in laboratory

In the laboratory, female *Euchaeta concinna* fed on both calanoid and cyclopoid copepods. Daily predation rates increased with increasing prey concentrations (Fig. 3.7). Among the five tested prey copepods, daily predation rate was highest on *Paracalanus / Parvocalanus*, followed by *Acrocalanus*, *Oithona*, *Corycaeu* and *Oncaea* when prey was provided at concentration of 10 prey L^{-1}. No saturation of daily predation rate of *E. concinna* on preys of *Paracalanus / Parvocalanus*, *Acrocalanus* and *Oithona* were found at the tested prey concentrations, while that of about 2 prey $predator^{-1}$ day^{-1} on *Corycaeu* and *Oncaea* were found when the predators fed at prey concentration higher than 5 prey L^{-1}.

3.3.8 Predation impact

Digestion times of female *Euchaeta concinna* on *Acrocalanus* and *Paracalanus/Parvocalanus* were determined in laboratory at 18°C. Values ranged from 5.6 h for *Acrocalanus* to 5.3 h for *Paracalanus/Parvocalanus*. Feeding rates and predation impacts of female *E. concinna* on these two groups of prey in S5 on 6–7 January 2005 were calculated (Tables 3.7 and 3.8). Daily predation impacts of female

E. concinna on *Acrocalanus* and *Paracalanus/Parvocalanus* were almost similar. On average, about 4.3% of the prey population was removed daily by female *E. concinna*.

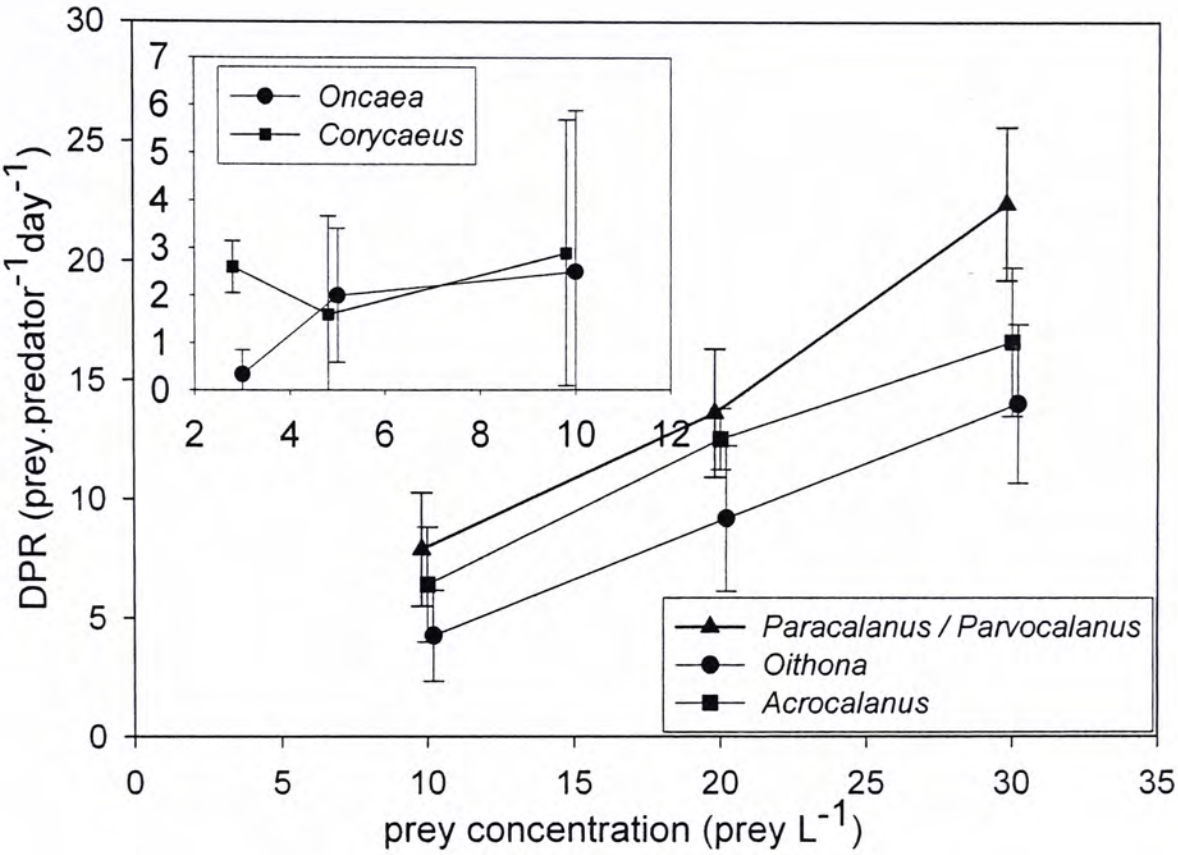

Fig.3.7. Laboratory feeding. Daily predation rates (DPR) of female adult *Euchaeta concinna* (mean ± S.D.) on prey copepod*s* at different prey concentrations in laboratory feeding experiments.

Table 3.7 Predation impact by adult female *Euchaeta concinna* on *Acrocalanus*. Digestion time (D) was estimated in the laboratory at 18°C. G_t is the number of prey per predator for predators collected at time interval t. Feeding rate (I_t) and predation impact (PI_t) at time interval (t) are calculated from $I_t = 4G_t / D$ and $PI_t = 100\ (I_t N_t / P_t)$ where N_t and P_t are the density of female *E. concinna* and prey, respectively. Daily predation impact (DPI) = $\Sigma\ PI_t$. Values in bracket denote SD.

t	D (h)	N_t (ind.m^{-3})	P_t (ind.m^{-3})	G_t (prey predator^{-1})	I_t (prey predator^{-1} time interval^{-1})	PI_t (% of prey removed time interval^{-1})
1200-1600 h		8.5 (2.2)	846 (120)	0 (0)	0	0
1600-2000 h		6.2 (0.1)	856 (346)	0.3 (0.5)	0.72	0.52
2000-2400 h	5.6	7.1 (3.7)	887 (159)	1.5 (1.1)	1.08	0.86
2400-0400 h	(1.5)	9.7 (0.1)	1184(166)	1.7 (0.9)	1.20	0.98
0400-0800 h		9.9 (0.5)	934 (90.7)	1.3 (0.5)	0.96	1.02
0800-1200 h		8.3 (1.2)	650 (71.2)	1.0 (0.6)	0.72	0.92
					DPI (% of prey removed per day)	4.30

Table 3.8 Predation impact of adult female *Euchaeta concinna* on *Paracalanus / Parvocalanus*. Digestion time (D) was estimated in the laboratory at 18 °C. G_t is the number of prey per predator for predators collected at time interval t. Feeding rate (I_t) and predation impact (PI_t) at time interval (t) are calculated from $I_t = 4G_t / D$ and $PI_t = 100\ (I_t N_t / P_t)$, where N_t and P_t are the abundance of female *E. concinna* and prey, respectively. Daily predation impact (DPI) = $\Sigma\ PI_t$. Values in bracket denote SD.

t	D (h)	N_t (ind.m^{-3})	P_t (ind.m^{-3})	G_t (prey predator^{-1})	I_t (prey predator^{-1} time interval^{-1})	PI_t (% of prey removed time interval^{-1})
1200-1600 h	5.3 (1.2)	8.5 (2.2)	866 (216)	0 (0)	0	0
1600-2000 h		6.2 (0.1)	1192 (159)	0 (0)	0	0
2000-2400 h		7.1 (3.7)	856 (57.6)	1.4 (0.3)	1.06	0.88
2400-0400 h		9.7 (0.1)	1121 (299)	1.0 (0.3)	0.76	0.66
0400-0800 h		9.9 (0.5)	930 (22.2)	2.0 (1.2)	1.52	1.62
0800-1200 h		8.3 (1.2)	763 (116)	0.5 (0.3)	1.01	1.10
					DPI (% of prey removed per day)	4.26

3.4 Discussion

3.4.1 Diel vertical distribution and diel feeding rhythm

Diel vertical distribution (DVM) was observed in both female and male *Euchaeta concinna* (Fig. 3.2). *Euchaeta concinna* stays in the deeper layer (> 15 m below water surface) in the daytime, ascends to shallower waters (0–15 m) after sunset, and returns to deeper waters after midnight. Other studies show that the congener *Pareuchaeta* also stays in the deeper layer during the day, and ascend to various depths at night (Yen 1985b; Bollens and Frost 1991). *Pareuchaeta norvegica* has been shown to perform DVM with amplitudes of hundreds of meters (Longhurst and Williams 1979; Yen 1985b; Mauchline 1992). *P. norvegica* in the Norwegian Sea stays in deep waters during both day and night (Fleddum *et al.* 2001), although a slightly shallower distributions at night has been reported by Skarra and Kaartvedt (2003) in a Norwegian fjord. In addition to the normal DVM, Kaartvedt *et al.* (2002) observed a bimodal vertical distribution for *P. norvegica* in another Norwegian fjord with a non-migrating deep population and a shallow population performing DVM and foraging in shallower waters in night. Fleddum *et al.* (2001) found that the vertical distribution is similar between males and females of *P. norvegica*. Their result is

similar to that found in this study. While vertical distribution of *P. elongata* (Bollens and Frost 1991; Mauchline 1995) and *P. norvegica* (Vestheim *et al.* 2005) is affected by ovigerity, no difference in vertical distribution was observed between ovigerous and non-ovigerous females of *E. concinna* in this study. In Mirs Bay, the main part of the *E. concinna* population stays at 10–15 m at noon where light level is very low. Below 15 m, reduction of light intensity with increasing depth becomes relatively small. This observation suggests that *E. concinna* adjusts its vertical distribution to achieve the optimal balance between energy cost of DVM and benefit of predator evasion.

Feeding activities of female *Euchaeta concinna* appear to coincide with the nocturnal ascent in the early part of the night. *E. concinna* females collected during the day have empty guts, but gut fullness increases after sunset and reaches a peak at midnight. Feeding activity is reduced after midnight. These observations show that *E. concinna* females have diel feeding rhythm and feed actively only at night. Nocturnal feeding has been reported in *Pareuchaeta* in laboratory (Yen 1982) and field studies (Kaartvedt *et al.* 2002; Skarra and Kaartvedt 2003). Diel feeding rhythm may also be independent of DVM. During the day, *E. concinna* stays at depths where prey density is low. Although the weighed mean depths (*WMD*) of the preferred prey *Acrocalanus*

and *Paracalanus/Parvocalanus* are significantly greater than that of female *E. concinna* during the day, the vertical distribution of the non-preferred prey *Canthocalanus* copepodids tends to overlap with that of *E. concinna* in both day and night. The absence of *Canthocalanus* in the guts of *E. concinna* in daytime indicates that the predators cease feeding in day and supports the conclusion that diel feeding rhythm is independent of DVM. Other studies have also demonstrated diel variations in gut contents in copepods regardless of DVM. Mackas and Bohrer (1976) found that the gut pigment fluorescence of both surface dwelling species and migrating species in the Bedford Basin reaches peak values only at night. Ishii (1990) reported independent diel feeding rhythm in two species of *Calanus* in the Bering Sea. *Calanus pacificus* in Dabob Bay performs diel vertical migration and enters the surface layer 2.5 hours before sunset, but its gut pigment content increases substantially only after sunset (Dagg *et al.* 1989). Diel feeding rhythm is widely considered to be a mechanism to avoid the accumulation of pigments in daytime (Kleppel *et al.* 1985; Dagg *et al.* 1989). As copepods are the major prey of the planktivorous fish, actively feeding copepods with pigmented guts are potentially more visible to visual predators. Laboratory and field experiments with the rainbow trout *Salmo gairdneri* have confirmed that visual predators select the most pigmented calanoid copepods as prey (Byron 1982). Bollens and Stearns (1992) reported that the gut fullness of *Acartia*

hudsonica is lower in the presence than in the absence of fish. *A. hudsonica* and *A. tonsa* reduced their gut fullness in the presence of fish exudates, and the response is observed only when light level is sufficient for visual predation (Cieri and Stearns 1999). These results suggest that the diel feeding rhythm in *E. concinna* is an adaptation to avoid visual predation.

3.4.2 Prey composition and selectivity

Gut content analysis reveals that small calanoid copepods are the major diet of female *Euchaeta concinna* and comprise ~40% of total gut content. The estimate is considered to be conservative as some crustacean remains (14 %) and unidentified item (17%) found in the guts may also be the remains of ingested copepods. Nevertheless, the importance of calanoid copepods as food of *E. concinna* is in accordance with previous findings on the natural diets of *Pareuchaeta* species (Øresland 1991; Øresland and Ward 1993). Copepods including *Metridia gerlachei*, *Calanoides acutus*, *Euchaeta* spp. *Oncaea* spp. and *Oithona* spp. make up 80–90% of all food items for adults and copepodids (C5) of *P. antarctica* (Øresland 1991). Øresland and Ward (1993) also reported that copepods form 46–99% of the diets of *P. antarctica*, *P. farrani*, *P. rasa* and *P. biloba* in South Georgia. *E. concinna* in Mirs

Bay feeds on small calanoid copepods including *Acrocalanus*, *Parvocalanus*, *Paracalanus* and copepodids of *Canthocalanus*, *Centropages* and *Subeucalanus*. *Acrocalanus*, *Paracalanus* and *Parvocalanus* are the preferred prey. Copepodids of *Canthocalanus* and other calanoid copepods are less preferred. In laboratory feeding experiments, Yen (1985a) found that prey size is an important factor for dietary selectivity by *Pareuchaeta norvegica* and the prosome length of preferred prey copepod is usually ~70% the length of the second basipodal segment of the maxilliped of the predator. A similar proportion of 65% was found for *P. antarctica,* which exhibited the highest feeding rates on copepods with prosome length of 1.2 mm (Yen 1991). For female *E. concinna*, the prosome length of *Acrocalanus* (~ 0.6–0.7 mm) is about 65–75% the length of the second basipodal segment of the maxilliped (~ 0.92 mm). Therefore, this observation agrees with the optimal prey size as proposed by Yen (1985a). Alternatively, the prosome lengths of *Paracalanus* and *Parvocalanus* (~ 0.3–0.4 mm) are only 33–40% of the length of the second basipodal segment of the maxilliped of female *E. concinna.* Using this relationship, it is expected that these smaller copepods may be suitable prey for the smaller later copepodid stages of *E. concinna* (C4 and C5). Also, the prosome length of the less preferred *Canthocalanus* copepodids (~ 0.8–1.0 mm) is ~85% the length of the second basipodal segment of the maxilliped of the predator.

It is interesting to note that female *Euchaeta concinna* does not feed on cyclopoid copepods, although laboratory feeding experiments showed that the females did feed on *Oithona*, *Oncaea* and *Corycaeus* but at a much lower feeding rate as compared to the preferred prey, *Acrocalanus* and *Paracalanus / Parvocalanus*, when tested with single prey experiments. Small cyclopoids copepods including *Oithona* and *Oncaea* have been found in the gut of *Pareuchaeta antarctica* and may even be the major prey of this predatory copepods, especially in the copepodid stages (Hopkins 1985; Øresland 1991; Øresland and Ward 1993). Yen (1985a) found in laboratory experiments that cyclopoids *Oithona* and *Corycaeus* are not the preferred prey of *P. Antarctica*. She suggested that the intermittent and darting movement of cyclopoids allow these small copepods to be less easily detected by tactile predators. The copepod community in Mirs Bay is dominated by calanoid copepods (> 80% of total copepod population) and *Oithona* and *Oncaea* species comprise only about 7% and 5%, respectively of the total copepod populations. The absence of cyclopoids in gut of female *E. concinna* may be because of their low abundance, small size (prosome length ~ 0.2–0.3 mm), and swimming behaviour.

3.4.3 Digestion time and feeding rate

Digestion time of female *Euchaeta concinna* on *Acrocalanus* and *Paracalanus/Parvocalanus* is 5.6 h and 5.3 h, respectively. Gut evacuation rates estimated for *Pareuchaeta norvegica* are 0.047 h^{-1} at 5°C and 0.080 h^{-1} at 15°C (Tönnesson *et al.* 2006). These correspond approximately to digestion times of 21 h and 12 h, respectively. These values are much longer than those estimated in this study at 18°C. Relationship between size of predator and digestion time in copepod is unclear, but some studies have shown that digestion time is independent of predator size. (Szyper 1978; Sullivan 1980). Conversely, it is known that digestion time is dependent on temperature (Kiørboe *et al.* 1982; Dam and Peterson 1988; Wlodarczyk *et al.* 1992; Uye and Yamamoto 1995; Li *et al.* 2004) as well as prey size (Martinussen and Båmstedt 2001). Higher water temperature in subtropical oceans allows higher metabolic rates and shorter digestion times for *E. concinna*. The prosome lengths of *Paracalanus* and *Pseudocalanus*, the major prey for *P. norvegica*, ranged from 0.5 to 0.8 mm (Tönnesson *et al.* 2006). In comparison, these copepods are slightly bigger than *Acrocalanus* with prosome length of ~0.7 mm and *Paracalanus/Parvocalanus* with prosome length of ~ 0.3–0.4 mm. Yen (1987) reported a considerably higher gut evacuation rate of 0.43 h^{-1} for *P. norvegica* feeding on cod larvae at 7.5 °C. This

corresponds to a very short digestion time of ~ 2 h. Fish larvae may be more digestible than crustaceans which contain chitinous exoskeleton.

Daily feeding rate of female *E. concinna* on *Acrocalanus* is ~4.7 prey predator^{-1}day^{-1}, while that on *Paracalanus/Parvocalanus* is ~4.4 prey predator^{-1}day^{-1}. Feeding rate varies with temperature and prey availability (Kiørboe *et al.* 1982; Yen 1982; Dam and Peterson 1988; Wlodarczyk *et al.* 1992). However, these values are in the range of experimental feeding rate of 3.6 prey predator^{-1}day^{-1} at 7–10 °C (Olsen *et al* 2000) and the in situ feeding rates of 1.4–5.2 prey predator^{-1}day at 5°C and 6.2–8.6 prey predator^{-1}day^{-1} at 15 °C (Tönnesson *et al.* 2006) for *P. norvegica*.

3.4.4 Predation impact

Euchaeta concinna females remove daily ~4.3% of the *Acrocalanus* and *Paracalanus/Parvocalanus* populations. The estimates are conservative as only predation by adult females has been considered. Predation impact by the entire *E. concinna* population on prey copepod assemblages may be much higher as *Paracalanus* and *Parvocalanus* are small enough to be eaten by copepodid stages C4 and C5 of *E. concinna* and the density of these two later copepodids stages in Mirs Bay

is often much higher (about four-fold) than that of adults. Yen (1991) found that the predation rates by C4 and C5 of *Pareuchaeta antartctica* on preferred prey of adults are 60% and 30%, respectively, of that of adults in laboratory feeding experiments. Assuming that digestion time of the adults is same as that of C4 and C5, about 13% of each the *Acrocalanus* and *Paracalanus/Parvocalanus* populations are estimated to be moved daily by the later copepopdid stages (C4 and C5) of *Euchaeta* population. To compare with other studies on predation impacts by predatory copepods, Tönnesson *et al.* (2006) reported predation impact of 2.0–6.5% on small copepods by *Pareuchaeta norvegica* in the Skagerrak. In other studies, predation impact by *Tortanus* spp. on small copepod populations ranges from 1% by in San Francisco Estuary (Hooff and Bollens 2004) to 2.7% in Fukuyama Harbour of Japan (Uye and Kayano 1994).

The trophic role of chaetognaths, an important invertebrate predator in the zooplankton, has been studied in many oceans. Predation impacts of 7.8 % in the eastern Mediterranean (Kehayias 2003), 6 % in the Mejillones Bay of Northern Chile (Giesecke and González 2004), and ~1 % in the Chesapeake Bay, (Bushing and Feigenbaum 1984), the Marion Island in the South Indian ocean (Froneman *et al.* 1998) and the Zanzibar Channel in the West Indian Ocean (Øresland 2000) have been reported. These findings suggest that carnivorous copepod *Euchaeta* may play a

significant role in regulating the populations of small copepods in the pelagic environments of Mirs Bay during winter and spring.

3.5 Conclusions

Both female and male *Euchaeta concinna* perform diel vertical migration (DVM) in Mirs Bay, by staying in the deeper layers in the day and ascending to shallower waters after sunset. Ovigerous and non-ovigerous females show similar diel vertical distribution. *E. concinna* females show diel feeding rhythm and the timing of nocturnal feeding coincides with the timing of upward migration at night.

Copepods comprise about 40% of the prey items found in the gut *Euchaeta concinna* females. *E. concinna* shows strong positive selection on *Acrocalanus*, weak positive selection on *Paracalanus/Parvocalanus*, and negative selection on *Canthocalanus* copepodids. Daily predation impacts of *E. concinna* females on *Acrocalanus* and *Paracalanus/Parvocalanus* are similar. For both groups of prey, ~4% of the population is removed daily by *E. concinna*. The predation impact of female *E. concinna* on small copepods estimated in this study is comparable to those reported for other carnivorous copepods and chaetognaths. It is concluded that *Euchaeta* may play a significant role in regulating the populations of small copepods in the pelagic ecosystems of Mirs Bay during winter and spring.

CHAPTER 4 CONCLUSIONS

This study examines the distribution, diel vertical migration and trophic role of the carnivorous copepod *Euchaeta* in subtropical pelagic ecosystems in the coastal waters of eastern Hong Kong. Three species of *Eucheata, E. concinna, E. rimana* and *E. plana* occur in the study area and *E. concinna* is the most abundant species. All species of *Euchaeta* show distinct seasonal distribution and dense populations are common only in winter and/or spring. Low density and lack of distinct pattern in cohort development suggests that *Euchaeta* species are not indigenous to local waters, but are transported into the study area by water masses from neighboring open seas. The distribution of this foreign genus is mostly restricted to offshore areas in Mirs Bay. The absence of *Euchaeta* in Tolo Harbour is probably because of (1) loss during the physical transport by ocean currents, and (2) higher fish predation pressure in Tolo Harbour.

Euchaeta concinna performs diel vertical distribution and diel feeding rhythm in Mirs Bay. The timing of nocturnal ascent coincides with the onset of nocturnal feeding. Both diel vertical migration and diel feeding rhythm are adaptations used by *Euchaeta* to minimize predation by visual predators in the shallow coastal water of

Hong Kong where fish density is high.

Gut content analysis reveals that small copepods are the main prey of female *Euchaeta concinna*. Small copepods including *Acrocalanus*, *Paracalanus* and *Parvocalanus* are the preferred prey, while slightly larger copepodids of *Canthocalanus* are not preferred. Daily predation impact of female *E. concinna* on the populations of *Acrocalanus* and *Paracalanus*/*Parvocalanus* is ~4%. As the density of C4 and C5 copepodids are often more than 10-fold higher than the density of adults, the total feeding impact by the entire population of *E. concinna* may be considerably higher. The predatory copepod *Euchaeta* may play an important role in regulating the populations of small copepods.

In conclusion, this study provides the information on the ecology of one of the most common and largest predatory copepod in the coastal waters of eastern Hong Kong. Our results suggest that predatory copepod of the genus *Euchaeta* plays an important trophic link between the primary grazers and the higher vertebrate predators in local marine ecosystem. More detailed study on the distribution of *Euchaeta* in relation to water circulation in the Chinese Coast is required to examine the speculation of water masses transport of *Euchaeta* population from the neighboring

oceans to local waters as suggested in the present study. Occurrence of this foreign copepod in the coastal waters of southern China may be indicative to the climatic changes of water current along the Chinese coast in the future. In addition, predation impact of the *Euchaeta* population on prey assemblage estimated in the present study is conservative as copepodids, which usually make up the larger component of the total population than adults, may contribute to a more significant impact. Indeed, further study on the trophic role of the copepodids of *Euchaeta* species is clearly in need in the future for our better understanding of the trophodynamic role of this predatory copepod in the pelagic food webs of the tropical and subtropical regions.

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Appendix 1 Comparison of mean water surface temperature between sampling station S1 – S6 over the entire sampling period.

One Way Analysis of Variance Wednesday, June 13, 2007, 12:33:24

Normality Test: Failed (P < 0.050)

Test execution ended by user request, ANOVA on Ranks begun

Kruskal-Wallis One Way Analysis of Variance on Ranks Wednesday, June 13, 2007, 12:33:24

Dependent Variable:

Group	N	Missing	Median	25%	75%
S1	42	6	25.240	19.300	28.555
S2	42	17	27.000	19.650	29.060
S3	42	3	22.990	18.957	28.235
S4	40	7	22.590	18.200	28.447
S5	40	16	25.850	20.950	28.805
S6	40	7	23.400	20.290	27.177

H = 3.535 with 5 degrees of freedom. (P = 0.618)

The differences in the median values among the treatment groups are not great enough to exclude the possibility that the difference is due to random sampling variability; there is not a statistically significant difference (P = 0.618)

Appendix 2 Comparison of mean water surface salinity between sampling station S1 – S6 over the entire sampling period.

One Way Analysis of Variance Wednesday, June 13, 2007, 12:42:55

Normality Test: Failed (P < 0.050)

Test execution ended by user request, ANOVA on Ranks begun

Kruskal-Wallis One Way Analysis of Variance on Ranks Wednesday, June 13, 2007, 12:42:55

Dependent Variable:

Group	N	Missing	Median	25%	75%
S1	35	0	32.300	31.025	34.000
S2	35	0	32.700	31.525	33.975
S3	35	0	33.200	31.800	33.850
S4	35	0	33.300	32.425	34.075
S5	35	0	33.300	32.275	34.375
S6	35	0	33.500	32.575	34.975

H = 7.612 with 5 degrees of freedom. (P = 0.179)

The differences in the median values among the treatment groups are not great enough to exclude the possibility that the difference is due to random sampling variability; there is not a statistically significant difference (P = 0.179)

Appendix 3 Comparison of mean water surface temperature between seasons (spring: Apr to May, summer: Jun to Sept, autumn: Oct to Nov and winter: Dec to Mar) at all sampling stations.

One Way Analysis of Variance Wednesday, June 13, 2007, 13:00:21

Normality Test: Passed (P = 0.307)

Equal Variance Test: Failed (P < 0.050)

Test execution ended by user request, ANOVA on Ranks begun

Kruskal-Wallis One Way Analysis of Variance on Ranks Wednesday, June 13, 2007, 13:00:21

Dependent Variable:

Group	N	Missing	Median	25%	75%
spring	7	0	24.877	22.464	26.496
summer	13	3	29.171	28.570	29.668
autumn	9	0	25.767	24.552	26.755
winter	15	0	17.867	16.290	20.239

H = 33.084 with 3 degrees of freedom. (P = <0.001)

The differences in the median values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference (P = <0.001)

To isolate the group or groups that differ from the others use a multiple comparison procedure.

All Pairwise Multiple Comparison Procedures (Dunn's Method) :

Comparison	Diff of Ranks	Q	P<0.05
summer vs winter	27.533	5.630	Yes
summer vs spring	14.643	2.480	No
summer vs autumn	11.056	2.009	Do Not Test
autumn vs winter	16.478	3.262	Yes
autumn vs spring	3.587	0.594	Do Not Test
spring vs winter	12.890	2.351	No

Note: The multiple comparisons on ranks do not include an adjustment for ties.

Appendix 4 Comparison of mean water surface salinity between seasons (spring: Apr to May, summer: Jun to Sept, autumn: Oct to Nov and winter: Dec to Mar) at all sampling stations.

One Way Analysis of Variance Wednesday, June 13, 2007, 12:56:07

Data source: seasonal temp & salinity in statistics_thesis

Normality Test: Passed (P = 0.459)

Equal Variance Test: Passed (P = 0.300)

Group Name	N	Missing	Mean	Std Dev	SEM
spring	7	0	32.250	1.292	0.489
summer	10	0	30.732	1.894	0.599
autumn	9	0	32.906	0.775	0.258
winter	15	0	34.318	0.952	0.246

Source of Variation	DF	SS	MS	F	P
Between Groups	3	79.547	26.516	16.400	<0.001
Residual	37	59.821	1.617		
Total	40	139.367			

The differences in the mean values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference (P = <0.001).

Power of performed test with alpha = 0.050: 1.000

All Pairwise Multiple Comparison Procedures (Tukey Test):

Comparisons for factor:

Comparison	Diff of Means	p	q	P	P<0.050
winter vs. summer	3.586	4	9.770	<0.001	Yes
winter vs. spring	2.068	4	5.025	0.006	Yes
winter vs. autumn	1.412	4	3.726	0.057	No
autumn vs. summer	2.174	4	5.262	0.004	Yes
autumn vs. spring	0.656	4	1.447	0.737	No
spring vs. summer	1.518	4	3.427	0.090	No

Appendix 5 Comparison of mean density of adult *Euchaeta concinna* between sampling station S1 – S6 over the entire sampling period.

One Way Analysis of Variance Wednesday, June 13, 2007, 22:16:36

Normality Test: Failed ($P < 0.050$)

Test execution ended by user request, ANOVA on Ranks begun

Kruskal-Wallis One Way Analysis of Variance on Ranks Wednesday, June 13, 2007, 22:16:36

Dependent Variable:

Group	N	Missing	Median	25%	75%
S6	36	0	0.359	0.000	1.319
S5	36	0	0.1000	0.000	0.510
S4	36	0	0.0579	0.000	0.593
S3	36	0	0.000	0.000	0.281
S2	36	0	0.000	0.000	0.121
S1	36	0	0.000	0.000	0.000

H = 28.987 with 5 degrees of freedom. (P = <0.001)

The differences in the median values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference (P = <0.001)

To isolate the group or groups that differ from the others use a multiple comparison procedure.

All Pairwise Multiple Comparison Procedures (Tukey Test):

Comparison	Diff of Ranks	q	P<0.05
S6 vs S1	2305.500	6.148	Yes
S6 vs S2	1548.500	4.129	Yes
S6 vs S3	1356.500	3.617	No
S6 vs S4	759.000	2.024	Do Not Test
S6 vs S5	651.500	1.737	Do Not Test
S5 vs S1	1654.000	4.411	Yes
S5 vs S2	897.000	2.392	No
S5 vs S3	705.000	1.880	Do Not Test
S5 vs S4	107.500	0.287	Do Not Test
S4 vs S1	1546.500	4.124	Yes
S4 vs S2	789.500	2.105	Do Not Test
S4 vs S3	597.500	1.593	Do Not Test
S3 vs S1	949.000	2.531	No
S3 vs S2	192.000	0.512	Do Not Test
S2 vs S1	757.000	2.019	Do Not Test

Note: The multiple comparisons on ranks do not include an adjustment for ties.

A result of "Do Not Test" occurs for a comparison when no significant difference is found between the two rank sums that enclose that comparison. For example, if you had four rank sums sorted in order, and found no significant difference between rank sums 4 vs. 2, then you would not test 4 vs. 3 and 3 vs. 2, but still test

4 vs. 1 and 3 vs. 1 (4 vs. 3 and 3 vs. 2 are enclosed by 4 vs. 2: 4 3 2 1). Note that not testing the enclosed rank sums is a procedural rule, and a result of Do Not Test should be treated as if there is no significant difference between the rank sums, even though one may appear to exist.

Appendix 6 Comparison of mean density of adult *Euchaeta rimana* between sampling station S1 – S6 over the entire sampling period.

One Way Analysis of Variance Wednesday, June 13, 2007, 22:19:46

Normality Test: Failed (P < 0.050)

Test execution ended by user request, ANOVA on Ranks begun

Kruskal-Wallis One Way Analysis of Variance on Ranks Wednesday, June 13, 2007, 22:19:46

Dependent Variable:

Group	N	Missing	Median	25%	75%
s6	19	0	0.0910	0.000	1.850
s5	19	0	0.0980	0.000	0.210
s4	19	0	0.000	0.000	0.206
s3	19	0	0.000	0.000	0.000
s2	19	0	0.000	0.000	0.000
s1	19	0	0.000	0.000	0.000

H = 42.783 with 5 degrees of freedom. (P = <0.001)

The differences in the median values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference (P = <0.001)

To isolate the group or groups that differ from the others use a multiple comparison procedure.

All Pairwise Multiple Comparison Procedures (Tukey Test):

Comparison	Diff of Ranks	q	P<0.05
s6 vs s1	758.000	5.261	Yes
s6 vs s2	758.000	5.261	Yes
s6 vs s3	659.000	4.574	Yes
s6 vs s4	405.000	2.811	No
s6 vs s5	87.000	0.604	Do Not Test
s5 vs s1	671.000	4.657	Yes
s5 vs s2	671.000	4.657	Yes
s5 vs s3	572.000	3.970	No
s5 vs s4	318.000	2.207	Do Not Test
s4 vs s1	353.000	2.450	No
s4 vs s2	353.000	2.450	Do Not Test
s4 vs s3	254.000	1.763	Do Not Test
s3 vs s1	99.000	0.687	Do Not Test
s3 vs s2	99.000	0.687	Do Not Test
s2 vs s1	0.000	0.000	Do Not Test

Note: The multiple comparisons on ranks do not include an adjustment for ties.

A result of "Do Not Test" occurs for a comparison when no significant difference is found between the two rank sums that enclose that comparison. For example, if you had four rank sums sorted in order, and found no significant difference between rank sums 4 vs. 2, then you would not test 4 vs. 3 and 3 vs. 2, but still test

4 vs. 1 and 3 vs. 1 (4 vs. 3 and 3 vs. 2 are enclosed by 4 vs. 2: 4 3 2 1). Note that not testing the enclosed rank sums is a procedural rule, and a result of Do Not Test should be treated as if there is no significant difference between the rank sums, even though one may appear to exist.

Appendix 7 Comparison of mean density of adult *Euchaeta plana* between sampling station S1 – S6 over the entire sampling period.

One Way Analysis of Variance Wednesday, June 13, 2007, 22:26:14

Normality Test: Failed (P < 0.050)

Test execution ended by user request, ANOVA on Ranks begun

Kruskal-Wallis One Way Analysis of Variance on Ranks Wednesday, June 13, 2007, 22:26:14

Dependent Variable:

Group	N	Missing	Median	25%	75%
s6	21	0	0.351	0.0895	0.620
s5	21	0	0.0980	0.000	0.247
s4	21	0	0.000	0.000	0.232
s3	21	0	0.000	0.000	0.116
s2	21	0	0.000	0.000	0.000
s1	21	0	0.000	0.000	0.000

H = 39.973 with 5 degrees of freedom. (P = <0.001)

The differences in the median values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference (P = <0.001)

To isolate the group or groups that differ from the others use a multiple comparison procedure.

All Pairwise Multiple Comparison Procedures (Tukey Test):

Comparison	Diff of Ranks	q	P<0.05
s6 vs s1	1133.000	6.771	Yes
s6 vs s2	960.500	5.740	Yes
s6 vs s3	874.000	5.223	Yes
s6 vs s4	560.000	3.346	No
s6 vs s5	363.500	2.172	Do Not Test
s5 vs s1	769.500	4.598	Yes
s5 vs s2	597.000	3.568	No
s5 vs s3	510.500	3.051	Do Not Test
s5 vs s4	196.500	1.174	Do Not Test
s4 vs s1	573.000	3.424	No
s4 vs s2	400.500	2.393	Do Not Test
s4 vs s3	314.000	1.876	Do Not Test
s3 vs s1	259.000	1.548	Do Not Test
s3 vs s2	86.500	0.517	Do Not Test
s2 vs s1	172.500	1.031	Do Not Test

Note: The multiple comparisons on ranks do not include an adjustment for ties.

A result of "Do Not Test" occurs for a comparison when no significant difference is found between the two rank sums that enclose that comparison. For example, if you had four rank sums sorted in order, and found

no significant difference between rank sums 4 vs. 2, then you would not test 4 vs. 3 and 3 vs. 2, but still test 4 vs. 1 and 3 vs. 1 (4 vs. 3 and 3 vs. 2 are enclosed by 4 vs. 2: 4 3 2 1). Note that not testing the enclosed rank sums is a procedural rule, and a result of Do Not Test should be treated as if there is no significant difference between the rank sums, even though one may appear to exist.

Appendix 8 Comparison of mean density of all copepodids (C1 – C5) between sampling station S1 – S6 over the entire sampling period.

One Way Analysis of Variance Wednesday, June 13, 2007, 23:49:01

Normality Test: Failed (P < 0.050)

Test execution ended by user request, ANOVA on Ranks begun

Kruskal-Wallis One Way Analysis of Variance on Ranks Wednesday, June 13, 2007, 23:49:01

Dependent Variable:

Group	N	Missing	Median	25%	75%
S6	40	0	3.575	1.592	11.399
S5	40	0	2.760	0.416	8.639
S4	40	0	1.024	0.250	4.064
S3	40	0	0.0554	0.000	1.158
S2	40	0	0.000	0.000	0.431
S1	40	0	0.000	0.000	0.000

H = 98.560 with 5 degrees of freedom. (P = <0.001)

The differences in the median values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference (P = <0.001)

To isolate the group or groups that differ from the others use a multiple comparison procedure.

All Pairwise Multiple Comparison Procedures (Tukey Test):

Comparison	Diff of Ranks	q	P<0.05
S6 vs S1	4605.000	10.488	Yes
S6 vs S2	3928.000	8.946	Yes
S6 vs S3	3315.500	7.551	Yes
S6 vs S4	1392.000	3.170	No
S6 vs S5	562.500	1.281	Do Not Test
S5 vs S1	4042.500	9.207	Yes
S5 vs S2	3365.500	7.665	Yes
S5 vs S3	2753.000	6.270	Yes
S5 vs S4	829.500	1.889	Do Not Test
S4 vs S1	3213.000	7.317	Yes
S4 vs S2	2536.000	5.776	Yes
S4 vs S3	1923.500	4.381	Yes
S3 vs S1	1289.500	2.937	No
S3 vs S2	612.500	1.395	Do Not Test
S2 vs S1	677.000	1.542	Do Not Test

Note: The multiple comparisons on ranks do not include an adjustment for ties.

A result of "Do Not Test" occurs for a comparison when no significant difference is found between the two rank sums that enclose that comparison. For example, if you had four rank sums sorted in order, and found

no significant difference between rank sums 4 vs. 2, then you would not test 4 vs. 3 and 3 vs. 2, but still test 4 vs. 1 and 3 vs. 1 (4 vs. 3 and 3 vs. 2 are enclosed by 4 vs. 2: 4 3 2 1). Note that not testing the enclosed rank sums is a procedural rule, and a result of Do Not Test should be treated as if there is no significant difference between the rank sums, even though one may appear to exist.

Appendix 9 Comparison of mean density of adult *Euchaeta concinna* between seasons (spring: Apr to May, summer: Jun to Sept, autumn: Oct to Nov and winter: Dec to Mar) at all sampling stations.

One Way Analysis of Variance Wednesday, June 13, 2007, 22:34:52

Normality Test: Failed (P < 0.050)

Test execution ended by user request, ANOVA on Ranks begun

Kruskal-Wallis One Way Analysis of Variance on Ranks Wednesday, June 13, 2007, 22:34:52

Dependent Variable:

Group	N	Missing	Median	25%	75%
spring	7	0	0.107	0.0191	1.004
summer	14	0	0.0154	0.000	0.0283
autumn	9	0	0.0204	0.0165	0.108
winter	15	0	0.397	0.163	2.033

H = 18.888 with 3 degrees of freedom. (P = <0.001)

The differences in the median values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference (P = <0.001)

To isolate the group or groups that differ from the others use a multiple comparison procedure.

All Pairwise Multiple Comparison Procedures (Dunn's Method) :

Comparison	Diff of Ranks	Q	P<0.05
winter vs summer	20.538	4.208	Yes
winter vs autumn	15.022	2.713	Yes
winter vs spring	10.110	1.682	No
spring vs summer	10.429	1.715	No
spring vs autumn	4.913	0.742	Do Not Test
autumn vs summer	5.516	0.983	Do Not Test

Note: The multiple comparisons on ranks do not include an adjustment for ties.

Appendix 10 Comparison of mean density of adult *Euchaeta rimana* between seasons (spring: Apr to May, summer: Jun to Sept, autumn: Oct to Nov and winter: Dec to Mar) at all sampling stations.

One Way Analysis of Variance *Wednesday, June 13, 2007, 22:39:58*

Normality Test: Failed ($P < 0.050$)

Test execution ended by user request, ANOVA on Ranks begun

Kruskal-Wallis One Way Analysis of Variance on Ranks *Wednesday, June 13, 2007, 22:39:58*

Dependent Variable:

Group	N	Missing	Median	25%	75%
spring	7	0	0.110	0.00708	0.630
summer	14	0	0.000	0.000	0.000
autumn	9	0	0.000	0.000	0.000
winter	15	0	0.0350	0.000	0.113

$H = 14.966$ with 3 degrees of freedom. ($P = 0.002$)

The differences in the median values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference ($P = 0.002$)

To isolate the group or groups that differ from the others use a multiple comparison procedure.

All Pairwise Multiple Comparison Procedures (Dunn's Method) :

Comparison	Diff of Ranks	Q	P<0.05
spring vs summer	15.500	2.549	No
spring vs autumn	15.476	2.338	Do Not Test
spring vs winter	3.676	0.611	Do Not Test
winter vs summer	11.824	2.423	Do Not Test
winter vs autumn	11.800	2.131	Do Not Test
autumn vs summer	0.0238	0.00424	Do Not Test

Note: The multiple comparisons on ranks do not include an adjustment for ties.

Appendix 11 Comparison of mean density of adult *Euchaeta plana* between seasons (spring: Apr to May, summer: Jun to Sept, autumn: Oct to Nov and winter: Dec to Mar) at all sampling stations.

One Way Analysis of Variance Wednesday, June 13, 2007, 22:43:33

Normality Test: Failed ($P < 0.050$)

Test execution ended by user request, ANOVA on Ranks begun

Kruskal-Wallis One Way Analysis of Variance on Ranks Wednesday, June 13, 2007, 22:43:33

Dependent Variable:

Group	N	Missing	Median	25%	75%
spring	7	0	0.137	0.0318	0.377
summer	14	0	0.000	0.000	0.000
autumn	9	0	0.000	0.000	0.000
winter	15	0	0.0874	0.0340	0.187

H = 27.392 with 3 degrees of freedom. (P = <0.001)

The differences in the median values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference (P = <0.001)

To isolate the group or groups that differ from the others use a multiple comparison procedure.

All Pairwise Multiple Comparison Procedures (Dunn's Method) :

Comparison	Diff of Ranks	Q	P<0.05
winter vs autumn	20.467	3.696	Yes
winter vs summer	18.324	3.754	Yes
winter vs spring	1.110	0.185	No
spring vs autumn	19.357	2.925	Yes
spring vs summer	17.214	2.831	Yes
summer vs autumn	2.143	0.382	No

Note: The multiple comparisons on ranks do not include an adjustment for ties.

Appendix 12 Comparison of mean density of all copepodids (C1 – C5) between seasons (spring: Apr to May, summer: Jun to Sept, autumn: Oct to Nov and winter: Dec to Mar) at all sampling stations.

One Way Analysis of Variance Thursday, June 14, 2007, 0:00:57

Normality Test: Failed ($P < 0.050$)

Test execution ended by user request, ANOVA on Ranks begun

Kruskal-Wallis One Way Analysis of Variance on Ranks Thursday, June 14, 2007, 0:00:57

Dependent Variable:

Group	N	Missing	Median	25%	75%
spring	7	0	1.648	0.788	3.384
summer	14	0	0.335	0.0708	0.464
autumn	9	0	1.293	0.439	2.292
winter	15	0	5.320	1.287	18.770

H = 21.051 with 3 degrees of freedom. (P = <0.001)

The differences in the median values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference (P = <0.001)

To isolate the group or groups that differ from the others use a multiple comparison procedure.

All Pairwise Multiple Comparison Procedures (Dunn's Method) :

Comparison	Diff of Ranks	Q	P<0.05
winter vs summer	22.138	4.536	Yes
winter vs autumn	10.511	1.898	No
winter vs spring	6.924	1.152	Do Not Test
spring vs summer	15.214	2.502	No
spring vs autumn	3.587	0.542	Do Not Test
autumn vs summer	11.627	2.072	Do Not Test

Note: The multiple comparisons on ranks do not include an adjustment for ties.

Appendix 13 Comparison of mean total density of female adult *Euchaeta concinna* between sampling times (1200, 1600, 2000, 2400, 0400 and 0800 h) on 6 -7 January 2005.

One Way Analysis of Variance Thursday, June 21, 2007, 12:22:37

Sampling time	N	Missing	Mean	Std Dev	SEM
1200 h	2	0	12.535	3.603	2.548
1600 h	2	0	11.924	2.450	1.732
2000 h	2	0	9.987	2.882	2.038
2400 h	2	0	14.123	0.665	0.470
0400 h	2	0	13.011	0.829	0.586
0800 h	2	0	11.258	0.745	0.527

Source of Variation	DF	SS	MS	F	P
Between Groups	5	20.607	4.121	0.853	0.560
Residual	6	28.978	4.830		
Total	11	49.585			

The differences in the mean values among the treatment groups are not great enough to exclude the possibility that the difference is due to random sampling variability; there is not a statistically significant difference (P = 0.560).

Power of performed test with alpha = 0.050: 0.051

The power of the performed test (0.051) is below the desired power of 0.800.
Less than desired power indicates you are less likely to detect a difference when one actually exists.
Negative results should be interpreted cautiously.

Appendix 14 Comparison of mean gut fullness of female adult *Euchaeta concinna* between sampling depths (0 – 5 m, 5 – 10 m, 10 – 15 m, 15 – 20 m and 20 -25 m) and sampling times (1200, 1600, 2000, 2400, 0400 and 0800 h).

Two Way Analysis of Variance Monday, April 18, 2005, 16:05:44

General Linear Model (No Interactions)

Dependent Variable: gut fullness

Normality Test: Passed (P = 0.066)

Equal Variance Test: Passed (P = 1.000)

Source of Variation	DF	SS	MS	F	P
Sampling time	5	0.700	0.140	8.188	<0.001
Sampling depth	5	0.0426	0.00853	0.498	0.774
Residual	25	0.428	0.0171		
Total	35	1.171	0.0334		

The difference in the mean values among the different levels of sampling time is greater than would be expected by chance after allowing for effects of differences in sampling depth. There is a statistically significant difference (P = <0.001). To isolate which group(s) differ from the others use a multiple comparison procedure.

The difference in the mean values among the different levels of sampling depth is not great enough to exclude the possibility that the difference is just due to random sampling variability after allowing for the effects of differences in sampling time. There is not a statistically significant difference (P = 0.774).

Power of performed test with alpha = 0.0500: for time : 0.996
Power of performed test with alpha = 0.0500: for depth : 0.0500

Least square means for sampling time:

Group	Mean
1200 h	0.0262
1600 h	0.0768
2000 h	0.249
2400 h	0.435
0400 h	0.137
0800 h	0.0709

Std Err of LS Mean = 0.0534

Least square means for sampling depth :

Group	Mean
0-5 m	0.169
5-10 m	0.234
10-15 m	0.126
15-20 m	0.138
20-25 m	0.160
0-25 m	0.169

Std Err of LS Mean = 0.0534

All Pairwise Multiple Comparison Procedures (Holm-Sidak method):
Overall significance level = 0.05

Comparisons for factor: **sampling time**

Comparison	**Diff of Means**	**t**	**Unadjusted P**	**Critical Level**	**Significant?**
2400 h vs. 1200 h	0.409	5.415	0.0000128	0.003	Yes
2400 h vs. 0800 h	0.364	4.824	0.0000588	0.004	Yes
2400 h vs. 1600 h	0.358	4.745	0.0000722	0.004	Yes
2400 h vs. 0400 h	0.298	3.946	0.000569	0.004	Yes
2000 h vs. 1200 h	0.223	2.953	0.00676	0.005	No
2400 h vs. 2000 h	0.186	2.462	0.0210	0.005	No
2000 h vs. 0800 h	0.178	2.361	0.0263	0.006	No
2000 h vs. 1600 h	0.172	2.282	0.0312	0.006	No
2000 h vs. 0400 h	0.112	1.484	0.150	0.007	No
0400 h vs. 1200 h	0.111	1.469	0.154	0.009	No
0400 h vs. 0800 h	0.0663	0.877	0.389	0.010	No
0400 h vs. 1600 h	0.0603	0.799	0.432	0.013	No
1600 h vs. 1200 h	0.0506	0.671	0.509	0.017	No
0800 h vs. 1200 h	0.0447	0.592	0.559	0.025	No
1600 h vs. 0800 h	0.00596	0.0790	0.938	0.050	No

Appendix 15 Comparison of Weigh Mean Depth (*WMD*) between female adult *Euchaeta concinna* and other copepods (*Paracalanus / Parvocalauns, Acrocalanus* and *Canthocalanus* copepodid) in daytime (1200, 1600 and 0800 h).

One Way Analysis of Variance Friday, June 15, 2007, 13:25:49

Group Name	N	Missing	Mean	Std Dev	SEM	
(1) *E. concinna*	6	0	16.843	1.344	0.549	
(2) *Acrocalanus*	6		0	9.841	3.404	1.390
(3) *Paracalanus/Parvocalanus*	6		0	9.905	1.126	0.460
(4) *Canthocalanus* copepodid	6		0	15.523	0.758	0.309

Source of Variation	DF	SS	MS	F	P
Between Groups	3	244.116	81.372	21.364	<0.001
Residual	20	76.176	3.809		
Total	23	320.292			

The differences in the mean values among the treatment groups are greater than would be expected by chance; there is a statistically significant difference (P = <0.001).

Power of performed test with alpha = 0.050: 1.000

All Pairwise Multiple Comparison Procedures (Tukey Test):

Comparisons for factor:

Comparison	Diff of Means	p	q	P	P<0.050
(1) vs. (2)	7.002	4	8.788	<0.001	Yes
(1) vs. (3)	6.938	4	8.708	<0.001	Yes
(1) vs. (4)	1.320	4	1.657	0.651	No
(4) vs. (2)	5.681	4	7.131	<0.001	Yes
(4) vs. (3)	5.618	4	7.051	<0.001	Yes
(3) vs. (2)	0.0635	4	0.0797	1.000	No

Appendix 16 Comparison of Weigh Mean Depth (*WMD*) between female adult *Euchaeta concinna* and other copepods (*Paracalanus* / *Parvocalauns*, *Acrocalanus* and *Canthocalanus* copepodid) in nighttime (2000, 2400 and 0400 h).

One Way Analysis of Variance Thursday, June 21, 2007, 10:44:50

Group Name	N	Missing	Mean	Std Dev	SEM	
E. concinna	6	0	12.769	3.102	1.266	
Acrocalanus	6	0	10.528	2.927	1.195	
Paracalanus/Parvocalanus	6	0	10.318	7.230	2.951	
Canthocalanus copepodid	6	0	12.228	13.431	5.483	

Source of Variation	DF	SS	MS	F	P
Between Groups	3	26.851	8.950	0.143	0.933
Residual	20	1254.276	62.714		
Total	23	1281.126			

The differences in the mean values among the treatment groups are not great enough to exclude the possibility that the difference is due to random sampling variability; there is not a statistically significant difference (P = 0.933).

Power of performed test with alpha = 0.050: 0.049

The power of the performed test (0.049) is below the desired power of 0.800.
Less than desired power indicates you are less likely to detect a difference when one actually exists.
Negative results should be interpreted cautiously.